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BRITISH · PTERIDOLOGICAL · SOCIETY

THE FERN GAZETTE

Proceedings of the International Pteridophyte Symposium

Ferns for the 21st Century

Royal Botanic Garden Edinburgh, Scotland, UK
12-16 July 2004

Part 2

EDITORS:
M. GIBBY, A. LEONARD, H. SCHNEIDER
& J.C. VOGEL

VOLUME 17 PART 4 2005

THE FERN GAZETTE is a journal of the British Pteridological Society and contains peer-reviewed papers on all aspects of pteridology.

Manuscripts may be submitted, and books etc. sent for review, to: Prof. M. Gibby, Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, EH3 5LR, UK
Telephone: 0131-248-2973 E-mail: FernGazette@eBPS.org.uk

Instructions for authors are on page 244 of this volume and also available at http://www.eBPS.org.uk

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THE FERN GAZETTE Volume 17 Part 3 was published on 15th September 2005

Published by THE BRITISH PTERIDOLOGICAL SOCIETY
c/o Department of Botany,
The Natural History Museum, London SW7 5BD, UK

Printed by Bishops Printers Limited
Fitzherbert Road, Farlington, Portsmouth, PO6 1RU, UK
www.bishops.co.uk

Cover design by Hazel Sims

British Pteridological Society
with
Royal Botanic Garden Edinburgh
Linnean Society of London

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GRAMMITIDACEAE (PTERIDOPHYTA) OF MOUNT JAYA, NEW GUINEA AND OTHER MONTANE MALESIAN LOCALITIES

B.S. PARRIS

Fern Research Foundation, 21 James Kemp Place, Kerikeri, Bay of Islands, New Zealand 0470 (Email: bsparris@igrin.co.nz)

Key words: Grammitidaceae, Pteridophyta, Mt Jaya, Mt Kinabalu, Seram, Gunung Mulu, Malesia

ABSTRACT

Mount Jaya (5000 m) in Papua (Indonesian New Guinea) is the highest mountain in Malesia and 56 species of Grammitidaceae are known from it. They are listed, together with their altitude ranges, habitat types and geographic distribution. Comparisons are made with Grammitidaceae of Murkele Ridge in Seram, Moluccas, Indonesia (3000 m, 55 species), Mount Kinabalu in Sabah, East Malaysia, Borneo (4100 m, 76 species) and Gunung Mulu, Sarawak, East Malaysia, Borneo (2400 m, 43 species). A Malesia-wide core of 23 grammitid species is identified.

INTRODUCTION

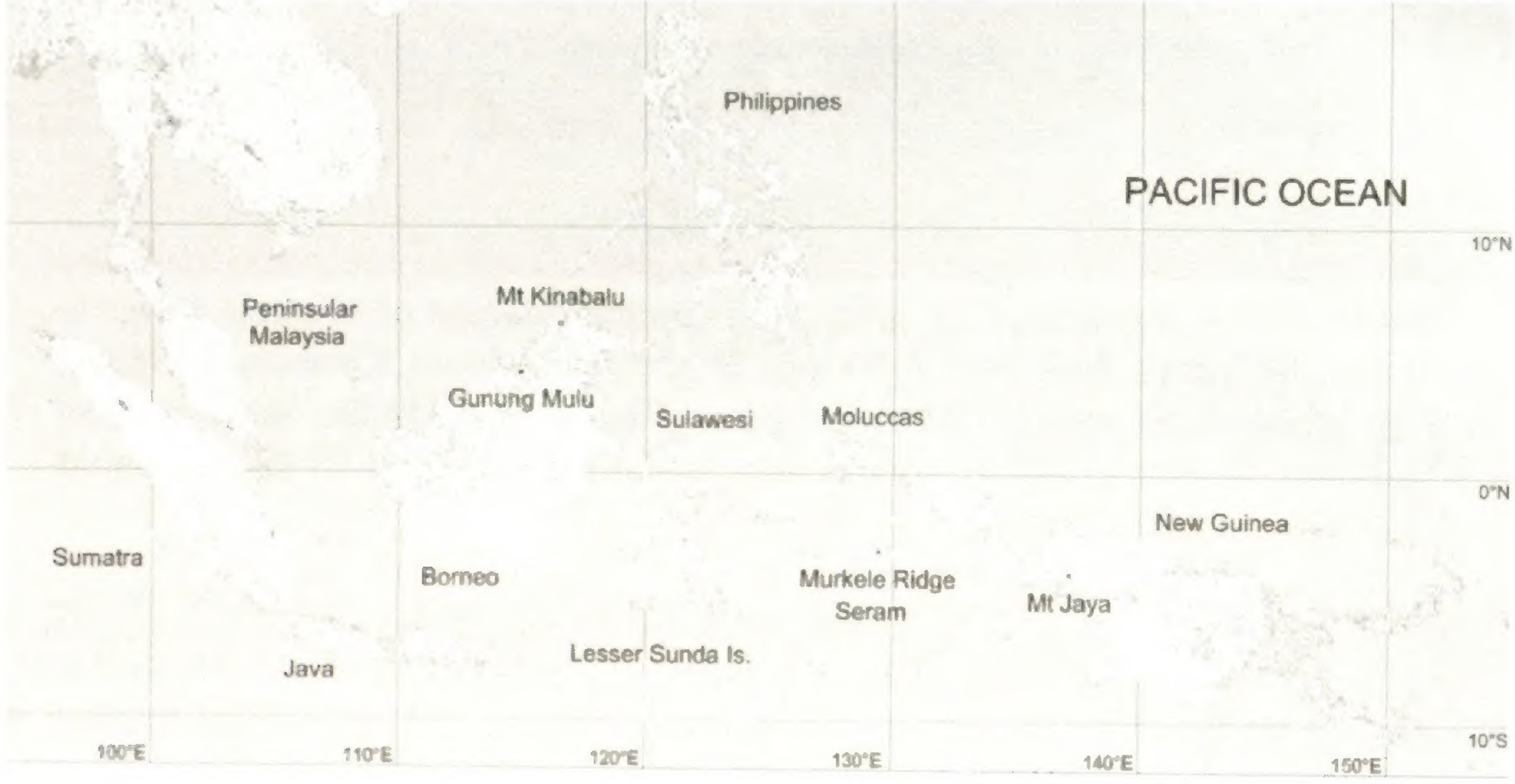
The limestone massif of Mount Jaya (c. 5000 m) in Papua (Indonesian New Guinea) is the highest peak in Southeast Asia. It is the only peak in the region high enough to support glaciers and has long been a magnet for biologists. Previous names for the mountain are Mount Carstensz and Punjak Sukarno. The Royal Botanic Gardens, Kew, has organised five botanical expeditions to the mountain during 1998 to 2000, during which many collections were made along an altitudinal transect on the southern side. A detailed description of the alpine flora of Mount Jaya (above 3000 m) is in preparation at the Royal Botanic Gardens, Kew (Johns *et al.* in prep.). While writing up the treatment of Grammitidaceae for this account, all relevant material collected on Mount Jaya was identified, not just that from high altitudes, and included specimens gathered by Kloss on the Wollaston expedition on the mountain during 1912-1913 and those collected by Miller in 1991 and 1992. Although nearly all of the available material has been collected from only the southern side of the mountain, it is of sufficient interest to document here in the following terms: 1) how many species?, 2) what are they?, 3) what are their altitude ranges?, 4) what vegetation types are they found in?, 5) where else do they occur?

Comprehensive collections of pteridophytes from specific localities are rare in Malesia, because many botanical collectors have specialised in gathering only flowering plants and have tended to overlook the smaller and more obscure species of pteridophytes, including most Grammitidaceae. There are only three other localities in Malesia where the fern flora, including Grammitidaceae, has been relatively well-collected over a wide altitudinal range: Mount Kinabalu Park in Sabah, East Malaysia, Borneo, Gunung Mulu National Park in Sarawak, East Malaysia and Murkele Ridge in Seram, Moluccas, Indonesia. More than 40 species are known from each of these localities and they provide a useful comparison with Mount Jaya. The following questions are relevant: 1) how much do the floras of the three areas have in common

with Mount Jaya?, 2) is there a distinct East Malesian element present on Mount Jaya and Murkele Ridge?, 3) is there a distinct West Malesian element on Mount Kinabalu and Gunung Mulu?, 4) is there a Malesia-wide group of species of predictable occurrence?, 5) do other pteridophytes show the same geographical distribution patterns and do they also have Malesia-wide species of predictable occurrence?

Map 1 shows the location of Mount Jaya, Murkele Ridge, Mount Kinabalu and Gunung Mulu.

Map 1. Malesia.



Most species of Grammitidaceae are epiphytes on trunks and branches of a variety of trees and shrubs, or on the trunks of *Cyathea* in alpine communities, often associated with bryophytes, and a few species, particularly those of subalpine habitats, are lithophytes.

Mount Jaya

56 species of Grammitidaceae are known from Mount Jaya. They are listed, together with their altitude range, vegetation types and distribution, in Table 1.

Tropical lowland rainforests are generally poor in members of Grammitidaceae, which are far more numerous above the average daily lower limits of cloud. On Mount Jaya only five (9%) species occur in lowland rainforest, which contains the tree genera *Chisocheton, Ficus, Myristica, Octomeles, Pometia* and *Vatica,* with undergrowth of ferns including tree ferns, *Arthropteris* and *Marattia*, and Gesneriaceae. All five species are also found in heath forest. Heath forest, the other lowland forest habitat on Mount Jaya, supports a surprisingly large number of species, 16 (29%). It occupies old Pleistocene outwash terraces at the foot of the mountain (R.J. Johns pers. comm.) and includes the trees *Alstonia spectabilis* R. Br., *Calophyllum, Casuarina, Dacrydium, Metrosideros* and *Vatica,* together with *Nepenthes, Davallia, Lecanopteris,* Hymenophyllaceae and Polypodiaceae. Two of the four Mount Jaya endemics, *Ctenopteris hymenophylloides* (also in lowland rainforest) and *Grammitis velutina,* occur here, together with two other species (*Ctenopteris nutans, Grammitis scabristipes)* disjunct from much higher altitudes in midmontane forest, upper montane

Table 1. Grammitidaceae of Mount Jaya.

Species	Altitude	Vegetation	Distribution
1. Acrosorus schlechteri (H.Christ) H.Christ	1700 m	LMF	New Guinea endemic
2. Calymmodon clavifer (Hook.) T.Moore	1200-2300 m	LMF MMF	Sumatra to New Guinea
3. C. cucullatus (Nees & Blume) C.Presl	2300-3500 m	MMF SA	Pen. Malaysia to Solomon Is.
4. C. fragilis Copel.	3800 m	SA	New Guinea endemic
5. C. mniodes Copel.	1800 m	MMF	Moluccas, New Guinea
6. C. ramifer Copel.	3600 m	SA	New Guinea endemic
7. Chrysogrammitis musgraviana (Baker) Parris	2500-2700 m	MMF UMF	SE Asia, Malesia to Vanuatu
8. Ctenopteris bipinnatifida (Baker) Copel.	2600-3600 m	UMF SA	New Guinea endemic
9. C. blechnoides (Grev.) W.H.Wagner & Grether	200-800 m	HF LF	S. India to Society Is.
10. C. denticulata (Blume) C.Chr. & Tardieu	1500-2300 m	LMF MMF	Indochina to New Guinea
11. C. fusca Copel.	3300-3800 m	SA	New Guinea endemic
12. C. hymenophylloides Parris	200-500 m	HF LF	Mount Jaya endemic
13. C. millefolia (Blume) Copel.	2000-2600 m	MMF	Sumatra to New Guinea
14. C. nutans (Blume) J.Sm.	500-3600 m	HF MMF SA	Pen. Malaysia to New Guinea
15. C. serrata Parris ined.	200-600 m	HF	Sulawesi to New Guinea
16. C. subsecundodissecta (Zoll.) Copel.	2200-2400 m	MMF	Java to New Caledonia
17. C. subulatipinna (Alderw.) Copel.	3200 m	SA	New Guinea endemic
18. Grammitis archboldii (C.Chr) Copel.	1800-2800 m	MMF UMF	New Guinea endemic

19. G. ceratocarpa Copel.	3500 m	SA	New Guinea endemic
20. G. clavata Parris	2400 m	MMF	Mount Jaya endemic
21. G. debilifolia Copel.	3600 m	SA	New Guinea endemic
22. G. dolichosora (Copel.) Copel.	500-600 m	HF LF	Borneo to New Guinea
23. G. frigida (Ridl.) Copel.	2300-4200 m	MMF SA	New Guinea endemic
24. G. hispida Copel.	2500 m	MMF	New Guinea endemic
25. G. interrupta (Baker) Copel.	2600 m	UMF	New Guinea endemic
26. G. intromissa (H.Christ) Parris	1800-3800 m	MMF SA	SE Asia to New Guinea
27. G. knutsfordiana (Baker) Copel.	800-2300 m	LMF MMF	Peninsular Malaysia to Fiji
28. G. locellata (Baker) Copel.	3500-3800 m	SA	Sumatra to New Guinea
29. G. loculosa (Alderw.) Copel.	500-2500 m	HF LMF MMF	New Guinea endemic
30. G. meijer-dreesii Copel.	3900 m	SA	New Guinea endemic
31. G. ornatissima (Rosenst.) Copel.	1900 m	MMF	Sumatra to New Guinea
32. G. padangensis (Baker) Copel.	2600-3900 m	MMF UMF SA	Sumatra to New Guinea
33. G. papuensis (Alderw.) Parris	800-2300 m	LMF MMF	Mount Jaya endemic
34. G. pleurogrammoides (Rosenst.) Copel.	600 m	HF	Moluccas to Solomon Is.
35. G. scabristipes (Baker) Copel.	400-3800 m	HF MMF SA	Sumatra to Vanuatu
36. G. sumatrana (Baker) Copel.	1700-2600 m	MMF UMF	Sumatra to New Guinea
37. G. velutina Parris	200-400 m	HF	Mount Jaya endemic
38. Prosaptia burbidgei (Baker) Parris	200 m	HF	Borneo to New Guinea
39. P. circumvallata (Rosenst.) Parris	2000-3400 m	MMF SA	New Guinea endemic
40. P. contigua (G.Forst.) C.Presl	1800-2300 m	MMF	S India to Marquesas Is.

41. P. davalliacea (F.Muell. & Baker) Copel.	3400-3700 m	SA	Pen. Malaysia to New Guinea
42. P. obliquata (Blume) Mett.	800 m	LMF	S India to New Guinea
43. P. papillata Parris ined.	800 m	LMF	New Guinea endemic
44. P. pensilis (Ridl.) Parris	1800 m	MMF	New Guinea endemic
45. P. venulosa (Blume ex Kunze) M.G.Price	2400 m	MMF	Java to New Guinea
46. Scleroglossum juncifolium Copel.	2700 m	UMF	New Guinea, Solomon Is.
47. S. pusillum (Blume) Alderw.	600 m	HF	Thailand to Solomon Is.
48. S. sulcatum (Kuhn) Alderw.	600 m	HF	Sri Lanka to Marquesas
49. Themelium allocotum (Alderw.) Parris	2300-3400 m	MMF SA	New Guinea endemic
50. T. fasciatum (Blume) Parris	200 m	HF LF	Sumatra to New Guinea
51. T. graminifolium (Copel.) Parris	2600 m	UMF	New Guinea endemic
52. T. yoderi (Copel.) Parris	1200-2400 m	LMF MMF	Philippines to Solomon Is.
53. Xiphopteris govidjoaensis (Brause) Copel.	500-600 m	HF LF	Pen. Malaysia to New Guinea
54. X. pseudospiralis (Alderw.) Parris	2400-2600 m	MMF UMF	New Guinea endemic
55. X. setulifera (Alderw.) Parris	500-600 m	HF	Pen. Malaysia to New Guinea
56. X. subpinnatifida (Blume) Copel.	1800-3600 m	MMF SA	Pen. Malaysia to New Guinea

HF, heath forest (200-600 m). LF, lowland rainforest (200-500 m). LMF, lower montane forest (800-1700 m). MMF, midmontane forest (1800-2800m). UMF, upper montane forest (2600-2700 m). SA, subalpine communities (3300-4200 m).

Note: altitude range 2800-3500 m not collected by Kew botanists because of precipitous nature of terrain along transect.

forest and subalpine communities. *Ctenopteris serrata, Grammitis pleurogrammoides, Prosaptia burbidgei, Scleroglossum pusillum, S. sulcatum* and *Xiphopteris setulifera* are known only from heath forest on Mount Jaya, but occur in other communities elsewhere in New Guinea and further afield in Malesia. The formation may exist elsewhere in New Guinea, but apparently no members of Grammitidaceae have been collected from it. Heath forest, also called kerangas, is known from Peninsular Malaysia, Borneo, and elsewhere in Malesia. It develops at low altitudes on very poor or thin soils over rock or in areas of impeded drainage and is characterised by straight, pole-like small to medium sized trees and an understorey including pitcher plants (*Nepenthes)*. Usually it contains very few, if any, species of Grammitidaceae.

Apart from heath forest, the most species-rich habitats on Mount Jaya are midmontane forest (28, 50%), and subalpine communities, with 19 species (21%). Lower montane and upper montane forests are less rich, each with 9 species (16%). Lower montane forest contains the fern *Selliguea* (no other information concerning the vegetation of lower montane forest is available on the specimen labels). The midmontane forest is dominated by *Nothofagus; Casuarina, Dacrydium, Fagraea,* Loranthaceae, *Macaranga, Papuacedrus, Rhododendron* and *Timonius* are also present together with the sedge *Mapania,* the ferns *Asplenium, Belvisia, Cyathea, Elaphoglossum* and *Loxogramme,* and shrubby Urticaceae. *Grammitis clavata* is the only Mount Jaya endemic in midmontane forest. Only eight species are restricted to midmontane forest, with another eight extending downward to lower montane forest and sometimes further, to heath forest and lowland rainforest, and 13 extending upwards to upper montane forest and sometimes to the subalpine communities. Upper montane forest is dominated by *Papuacedrus papuana* (F. Muell.) Li and *Podocarpus brassii* Pilg., with *Dicksonia, Drimys, Elaeocarpus, Nepenthes, Rapanea, Rhododendron, Sloanea* and *Utricularia. Grammitis interrupta, Scleroglossum juncifolium* and *Themelium graminifolium* are restricted to upper montane forest on Mount Jaya, but occur in other vegetation types elsewhere. Another five species occur in midmontane forest as well as upper montane forest, and two, *Ctenopteris bipinnatifida* and *Grammitis padangensis,* extend to the subalpine zone. The subalpine grasslands are dominated by *Cyathea* tree ferns, while the subalpine shrubland contains *Cyathea, Coprosma, Drimys, Rhododendron* and *Vaccinium,* and the subalpine forest contains *Dacrycarpus compactus* (Wassch.) de Laub. and *Podocarpus*. Nine species are restricted to subalpine habitats: *Calymmodon fragilis, C. ramifer, Ctenopteris fusca, C. subulatipinna, Grammitis ceratocarpa, G. debilifolia, G. locellata, G. meijer-dreesii* and *Prosaptia davalliacea.* With the exception of *G. locellata* and *P. davalliacea,* all are New Guinea endemics. While the nine species all occur on Mount Jaya at altitudes higher than that of the nearest subalpine site to New Guinea, Murkele Ridge (3000 m) in Seram, the two species that are widespread through Malesia, *G. locellata* and *P. davalliacea,* occur at lower altitudes on Murkele Ridge.

Several species found on Mount Jaya are infrequently collected and are known from very few localities. They include medium to high altitude Papua endemics known elsewhere only from Lake Habbema - *Grammitis hispida, Themelium allocotum,* Mount Trikora - *Ctenopteris fusca, G. meijer-dreesii*, and/or Mount Doorman, *C. subulatipinna, T. allocotum,* and Mount Goliath and Hellwig Mounts - *Xiphopteris pseudospiralis*. *Xiphopteris govidjoaensis* (syn. *X. exilis* Parris) is known from two other localities, Gunung Belumut in Peninsular Malaysia and Govidjoa in Papua New Guinea.

Four species (7%) are endemic to Mount Jaya; *Ctenopteris hymenophylloides*, *Grammitis clavata*, *G. papuensis* and *G. velutina*. Surprisingly, none occurs in the subalpine communities, as might be expected when considering that several other mountains in New Guinea have high altitude endemics, e. g. *Grammitis dictymioides* Copel, *G. habbemensis* Copel., *Xiphopteris antipodalis* Copel. (all Lake Habbema), *G. reptans* Parris (Mount Trikora), *G. montana* Parris, *G. trogophylla* Copel. (both Mount Sarawaket), *G. murrayana* (C.Chr.) Copel. (Wharton Range) and *G. salticola* Parris (Mount Giluwe) (Parris, 1983).

A number of other high altitude New Guinea species found on Mount Trikora and/or Lake Habbema, and elsewhere in Papua New Guinea, may be expected on Mount Jaya, including *Ctenopteris pendens* (Rosenst.) Copel., *C. whartoniana* (C.Chr.) Copel. and *Grammitis tomaculosa* Parris.

New Guinea endemic species are important on Mount Jaya, comprising 36% (20 species) of the total. While they occur in all of the vegetation types they are best represented in the high altitude subalpine communities, where they form 20% (11 species) of the total number of species. The largest number of species, 24 (43%) are Malesia-wide in the sense that they occur in both West Malesia and East Malesia, on both sides of Zollinger's line (see later) between Borneo and Sulawesi, sometimes extending into Thailand, Indochina and Taiwan to the north-west and into Melanesia (Solomon Islands, Vanuatu, New Caledonia and Fiji) to the south-east. A small group of species (4, 7%) is very wide-ranging, from South India to the Society Islands (*Ctenopteris blechnoides*), South India to the Marquesas Islands (*Prosaptia contigua*), Sri Lanka to the Marquesas Islands (*Scleroglossum sulcatum*) and from South India to New Guinea (*P. obliquata*). These four species are amongst the most common and widespread members of Grammitidaceae in the Asia-Malesia-Pacific region. Another four (7%) species are restricted to East Malesia; *Ctenopteris serrata* ranges from Sulawesi to New Guinea, *Calymmodon mniodes* is in the Moluccas and New Guinea, *Grammitis pleurogrammoides* extends from the Moluccas to the Solomon Islands and *Scleroglossum juncifolium* occurs in New Guinea and the Solomon Islands.

The grammitid flora of Mount Jaya inevitably invites comparison with that of Mount Kinabalu (4100 m) in Sabah, Borneo, East Malaysia, the highest peak between the Himalayas and Papua, and the two other areas sufficiently well-known to permit comparison of their grammitid floras: the Murkele Ridge, a limestone massif including Gunung Binaiya (3000 m) in Seram, Moluccas, Indonesia, and Gunung Mulu National Park (including Gunung Mulu, sandstone, 2400 m and Gunung Api, limestone, 1700 m) in Sarawak, Borneo, East Malaysia. It is useful to examine the composition of these montane grammitid floras with respect to Zollinger's line, which divides West Malesia, comprising Peninsular Malaysia, Sumatra, Java, Borneo, the Philippines and the Lesser Sunda Islands, from East Malesia, consisting of Sulawesi, the Moluccas and New Guinea, and separated by the Makassar Strait between Borneo and Sulawesi. Wallace's line is similar, but includes Bali, the westernmost of the Lesser Sunda Islands, in West Malesia, and the remaining Lesser Sunda Islands in East Malesia. As the Lesser Sunda Islands are considered a discrete botanical region, Zollinger's line is preferred to Wallace's line. Mount Kinabalu and Gunung Mulu National Park (subsequently referred to as Gunung Mulu) are in West Malesia, while Murkele Ridge and Mount Jaya are in East Malesia. Both Mount Kinabalu and Murkele Ridge have subalpine areas above the treeline, but Gunung Mulu is forested to its summit.

The Moluccas have been of biogeographical interest ever since Wallace (1869)

suggested that the region has been constantly receiving immigrants from New Guinea. Kato (1989a) also points out that the affinity of the fern flora of Seram at species level is with New Guinea to the east rather than with Sulawesi to the west. Parris (1993) notes that the endemic pteridophytes of Seram are derived on the whole from wide-ranging taxa or those from East Malesia, and that Seram is the end of the line for numerous species moving east from West Malesia and moving west from New Guinea. Grammitidaceae of Seram collected by the Japanese-Indonesian expeditions of 1983, 1985 and 1986 (but not those collected by Parris in 1987) have been listed (Kato & Parris, 1992), the pteridophyte flora of Mount Kinabalu has been documented (Parris *et al.*, 1992), and a checklist of pteridophytes of Gunung Mulu National Park has been compiled (Parris, unpublished). Numerous changes have been made to the taxonomy of Grammitidaceae in Seram and on Mount Kinabalu since the publications of Kato & Parris (1992) and Parris *et al.* (1992).

Murkele Ridge

55 species of Grammitidaceae are known from Murkele Ridge. They are listed, together with their altitude range, vegetation types and distribution, in Table 2.

It is useful to compare the grammitid floras of Mount Jaya and Murkele Ridge, the two East Malesian localities, which have very similar numbers of species, 56 in the former and 55 in the latter. 25 species are shared between the two, and nine of these are restricted to East Malesia. The remaining 16 are more widespread, occurring in East and West Malesia and sometimes beyond. Only *Ctenopteris serrata* extends throughout East Malesia from Sulawesi to New Guinea, so a well-defined widespread East Malesian endemic element is lacking in Grammitidaceae. Only one species, *Acrosorus friderici-et-pauli*, reaches its eastern limit of distribution on Murkele Ridge in Seram, but eight others, *Calymmodon mniodes*, *Ctenopteris whartoniana*, *Grammitis ahenobarba*, *G. collina*, *G. parva*, *G. pseudolocellata*, *G. subfasciata* and *Prosaptia engleriana*, reach their western limit in Seram, either on Murkele Ridge or slightly further to the north-west on Gunung Kobipoto (*G. collina*) or Gunung Roihelu (*G. parva*). They amply demonstrate Wallace's point (1869) that the Moluccas receive immigrants from New Guinea. In addition, some of the Murkele Ridge endemic species have obvious vicariants in New Guinea, e. g. *Ctenopteris themelioides* with *C. hipinnatifida*, and *Themelium pseudallocotum* with *T. allocotum*. The similarity in species numbers between Mount Jaya and the much lower Murkele Ridge is surprising, and the reasons for it are not obvious.

Comparisons between Murkele Ridge and the two West Malesian localities, Mount Kinabalu and Gunung Mulu, are interesting. 33 species are shared with Mount Kinabalu, more than are shared with Mount Jaya. They include seven widespread species collected on Gunung Mulu and known from New Guinea that are absent from Mount Jaya: *Calymmodon gracilis*, *C. pectinatus*, *C. reconditus*, *Ctenopteris brevivenosa*, *Grammitis adspersa*, *G. impressa*, *G. reinwardtii*. All are expected on Mount Jaya. 19 species are shared with Gunung Mulu and, with the exception of *Calymmodon conduplicatus*, all are also known from Mount Kinabalu.

31 species (56%) on Murkele Ridge are found in both East and West Malesia and another 5 (9%) extend well beyond Malesia, while 9 species (16%) occur in East Malesia and another 9 (16%) are endemic to Murkele Ridge. The amount of local endemism is much higher than on Mount Jaya, which has only four endemics. One might expect local endemism at high altitudes on Murkele Ridge, the highest part of the

Table 2. Grammitidaceae of Murkele Ridge.

Species	Altitude	Vegetation	Distribution
1. Acrosorus friderici-et-pauli (H.Christ) Copel.	1300-2000 m	LMF	SE Asia to Moluccas
2. A. vallatus Parris ined.	1700 m	LMF	Murkele Ridge endemic
3. Calymmodon binaiyensis Parris ined.	2800 m	SA	Murkele Ridge endemic
4. C. clavifer (Hook.) T.Moore	1700-2000 m	LMF	Sumatra to New Guinea
5. C. conduplicatus (Brause) Copel.	1200-2500 m	LMF UMF	Borneo to New Guinea
6. C. cucullatus (Nees & Blume) C.Presl	1800-2800 m	LMF UMF SA	Pen. Malaysia to Solomon Is.
7. C. gracilis (Fée) Copel.	1800 m	LMF	SE Asia to New Guinea
8. C. mniodes Copel.	1800 m	LMF	Moluccas, New Guinea
9. C. pectinatus Parris ined.	1600-1800 m	LMF	Java to New Guinea
10. C. reconditus Parris ined.	2500 m	UMF	Borneo to New Guinea
11. Chrysogrammitis musgraviana (Baker) Parris	1200-2000 m	LMF	SE Asia, Malesia to Vanuatu
12. Ctenopteris blechnoides (Grev.) W.H.Wagner & Grether	500-1300 m	LF LMF S.	India to Society Is.
13. C. brevivenosa (Alderw.) Holttum	2400 m	UMF	Thailand to Vanuatu
14. C. denticulata (Blume) C.Chr. & Tardieu	1200 m	LMF	Indochina to New Guinea
15. C. millefolia (Blume) Copel.	1800-2000 m	LMF	Sumatra to New Guinea
16. C. nutans (Blume) J.Sm.	1800-2900 m	LMF UMF	Pen. Malaysia to New Guinea
17. C. seramensis Parris ined.	1600 m	LMF	Murkele Ridge endemic
18. C. serrata Parris ined.	600-2000 m	LMF	Sulawesi to New Guinea

19. C. subsecundodissecta (Zoll.) Copel.	1300 m	LMF	Java to New Caledonia
20. C. themelioides Parris ined.	2000-2800 m	LMF UMF SA	Murkele Ridge endemic
21. C. whartoniana (C.Chr.) Copel.	2900 m	SA	Moluccas, New Guinea
22. Grammitis adspersa (Blume) Blume	1600 m	LMF	SE Asia to Fiji
23. G. ahenobarba Parris	1600 m	LMF	Moluccas, New Guinea
24. G. caespitosa Blume	2100 m	LMF	Sumatra to New Guinea
25. G. collina Parris	1400 m	LMF	Moluccas, New Guinea
26. G. dolichosora (Copel.) Copel.	800-2000 m	LMF	Borneo to New Guinea
27. G. impressa Copel.	1300 m	LMF	Sumatra to New Guinea
28. G. intromissa (H.Christ) Parris	1600-2000 m	LMF	Taiwan to New Guinea
29. G. kanikehensis Parris ined.	600 m	LMF	Murkele Ridge endemic
30. G. knutsfordiana (Baker) Copel.	2000 m	LMF	Peninsular Malaysia to Fiji
31. G. locellata (Baker) Copel.	2800-2900 m	SA	Sumatra to New Guinea
32. G. manuselensis Parris ined.	600 m	LMF	Murkele Ridge endemic
33. G. mollis Parris ined.	1700 m	LMF	Borneo to Moluccas
34. G. padangensis (Baker) Copel.	1800-2000 m	LMF	Sumatra to New Guinea
35. G. parva (Brause) Copel.	1800-2900 m	LMF UMF SA	Moluccas, New Guinea
36. G. pseudolocellata Parris	2900 m	SA	Moluccas, New Guinea
37. G. reinwardtii Blume	700-2000 m	LMF	Sri Lanka to Solomon Is.
38. G. scabristipes (Baker) Copel.	2200-2900 m	UMF SA	Sumatra to Vanuatu
39. G. subfasciata (Rosenst.) Copel .	1400-1900 m	LMF	Moluccas, New Guinea
40. G. sumatrana (Baker) Copel.	1300-2000 m	LMF	Sumatra to New Guinea

41. G. tehoruensis M.Kato & Parris	1300 m	LMF	Murkele Ridge endemic
42. Prosaptia contigua (G.Forst.) C.Presl	700-2000 m	LMF	S India to Marquesas Is.
43. P. davalliacea (F.Muell. & Baker) Copel.	2800-2900 m	SA	Pen. Malaysia to New Guinea
44. P. engleriana (Brause) Copel.	600-800 m	LMF	Moluccas, New Guinea
45. P. obliquata (Blume) Mett.	600-2000 m	LMF	S India to New Guinea
46. P. seramensis Parris ined.	1800-2000 m	LMF	Murkele Ridge endemic
47. P. subglabra (M.Kato & Parris) Parris	1300-1600 m	LMF	Moluccas endemic
48. P. venulosa (Blume ex Kunze) M.G.Price	2100 m	LMF	Java to New Guinea
49. Scleroglossum pusillum (Blume) Alderw.	1000-1300 m	LMF	Thailand to Solomon Is.
50. S. sulcatum (Kuhn) Alderw.	1000-1300 m	LMF	Sri Lanka to Marquesas
51. Themelium pseudallocotum Parris ined.	1300 m	LMF	Murkele Ridge endemic
52. T. taxodioides (Baker) Parris	2200 m	UMF	Borneo to New Guinea
53. T. yoderi (Copel.) Parris	1800-2000 m	LMF	Philippines to Solomon Is.
54. Xiphopteris setulifera (Alderw.) Parris	900-1000 m	LMF	Pen. Malaysia to New Guinea
55. X. subpinnatifida (Blume) Copel.	1800 m	LMF	Pen. Malaysia to New Guinea

LF, lowland forest (600 m). LMF, lower montane forest (600-2100 m). UMF, upper montane forest (2100-2500 m). SA, subalpine communities (2400-3000 m).

Moluccas and the only part of the region to be above the tree line, but only *Calymmodon binaiyensis* is restricted to subalpine habitats. *Ctenopteris themelioides* ranges from lower montane forest to subalpine habitats while the other local endemics are all found in lower montane forest. Only one species, *Prosaptia subglabra*, is endemic to the Moluccas.

Mount Kinabalu

76 species of Grammitidaceae are known from Mount Kinabalu. They are listed, together with their altitude range, vegetation types and distribution, in Table 3.

Mount Kinabalu and Mount Jaya make an interesting contrast. The former has far more species of Grammitidaceae, 76, than the latter, with 56. Mount Kinabalu has a long history of botanical collecting, however, over more than a century, which may explain its species richness in part (Parris *et al.*, 1992). It should be noted, however, that nine species have not been collected on the mountain in the last 60 years (Parris, 2001) and may well be locally extinct. 23 species occur on both mountains; all of them, except *Themelium fasciatum*, are also found on Murkele Ridge, and 10 of them are also found on Gunung Mulu. Mount Kinabalu has nine endemic species of Grammitidaceae (16%), more than double the number found on Mount Jaya. As with Murkele Ridge, one might expect the endemic species to be associated with the high altitude vegetation communities above the tree line, but only *Grammitis kinabaluensis* extends above the tree line, and it also occurs in lower montane and mid-montane forest. *Grammitis graniticola*, *G. muscicola* and *G. nubicola* are restricted to upper montane forest, while *Calymmodon innominatus* and *Grammitis ramicola* are found only in lower montane forest and *Calymmodon kinabaluensis*, *Grammitis havilandii* and *G. ultramaficola* occur in both lower montane and upper montane forest. 44 species (58%) are Malesian-wide, a higher number and percentage than for either Mount Jaya or Murkele Ridge. Another eight species (11%) extend well beyond Malesia. 10 species are restricted to West Malesia, six of which are also found on Gunung Mulu. The West Malesian *Ctenopteris fuscata* occurs at high altitudes on Mount Kinabalu (3000-3800 m) and is not found on Gunung Mulu (2400 m), but *Grammitis congener* (1100-2500 m) and *Themelium curtisii* (1400-2400 m) are absent from Gunung Mulu, but may be expected. *Xiphopteris nudicarpa* occurs on ultramafic rocks on Mount Kinabalu and on Palawan Island in the Philippines. Ultramafic rocks, and *X. nudicarpa*, are absent from Gunung Mulu. Five species are endemic to Borneo and all are shared with Gunung Mulu.

Gunung Mulu

43 species of Grammitidaceae are known from Gunung Mulu. They are listed, together with their altitude range, vegetation types and distribution, in Table 4.

Gunung Mulu is lower than Mount Jaya, Murkele Ridge and Mount Kinabalu, and lacks vegetation communities above the tree line. It has no endemic species, and 36 of its 43 species are also found on Mount Kinabalu. 22 species (51%) are Malesian-wide and five (12%) range well beyond Malesia. The nine West Malesian species (21%) all occur on Mount Kinabalu. Seven species are endemic to Borneo; five also occur on Mount Kinabalu, but *Scleroglossum crassifolium* and *Themelium sarawakense* are not known there.

In Table 5 the geographic distribution of Grammitidaceae on Mount Jaya, Murkele Ridge, Mount Kinabalu and Gunung Mulu is summarised.

Table 3. Grammitidaceae of Mount Kinabalu.

Species	Altitude	Vegetation	Distribution
1. Acrosorus friderici-et-pauli (H.Christ) Copel.	1500-1900 m	LMF	SE Asia to Moluccas
2. A. streptophyllus (Baker) Copel.	800-1900 m	HF LMF	Thailand to Philippines
3. Calymmodon atrichus Copel.	1800-3400 m	LMF UMF	Borneo to New Guinea
4. C. borneensis Parris ined.	1500-3000 m	LMF UMF	Borneo endemic
5. C. clavifer (Hook.) T.Moore	1500-2600 m	LMF	Sumatra to New Guinea
6. C. cucullatus (Nees & Blume) C.Presl	2200-3000 m	LMF UMF	Pen. Malaysia to Solomon Is.
7. C. gracilis (Fée) Copel.	1200-3000 m	LMF UMF	SE Asia to New Guinea
8. C. hygroscopicus Copel.	1400-2100 m	LMF	Java to New Guinea
9. C. innominatus Parris ined.	2400 m	LMF	Mount Kinabalu endemic
10. C. kinabaluensis Parris ined.	1500-2800 m	LMF UMF	Mount Kinabalu endemic
11. C. luerssenianus (Domin) Copel.	1500-2400 m	LMF	SE Asia to Solomon Is.
12. C. muscoides (Copel.) Copel.	1500 m	LMF	Java to Philippines
13. C. pectinatus Parris ined.	1500-2500 m	LMF	Java to New Guinea
14. C. reconditus Parris ined.	1500-3100 m	LMF UMF	Borneo to New Guinea
15. Chrysogrammitis glandulosa (J.Sm.) Parris	1500 m	LMF	Sri Lanka to Philippines
16. C. musgraviana (Baker) Parris	1400-2100 m	LMF	SE Asia to Vanuatu
17. Ctenopteris blechnoides (Grev.) W.H.Wagner & Grether	800-1000 m	HF	S. India to Society Is.
18. C. brevivenosa (Alderw.) Holttum	1400-3000 m	LMF UMF	Thailand to Vanuatu
19. C. denticulata (Blume) C.Chr. & Tardieu	1200-1800 m	LMF	Indochina to New Guinea
20. C. fuscata (Blume) Kunze	3000-3800 m	UMF SA	Thailand to Philippines
21. C. inconspicua (Blume) Copel.	1700 m	LMF	Pen. Malaysia to Philippines
22. C. millefolia (Blume) Copel.	1800 m	LMF	Sumatra to New Guinea
23. C. minuta (Blume) Holttum	1400 m	LMF	Pen. Malaysia to Philippines
24. C. mollicoma (Nees & Blume) Kunze	1500-2900 m	LMF UMF	SE Asia to New Guinea
25. C. nutans (Blume) J.Sm.	2600-3800 m	UMF SA	Pen. Malaysia to New Guinea

26. C. repandula (Mett.) C.Chr. & Tardieu	2700 m	UMF	Sri Lanka to Solomon Is.
27. C. subminuta (Alderw.) Holttum	1400-2000 m	LMF	Sumatra to Borneo
28. C. subsecundodissecta (Zoll.) Copel.	1700-2400 m	LMF	Java to New Caledonia
29. Grammitis adspersa (Blume) Blume	1500 m	LMF	SE Asia to Fiji
30. G. bongoensis (Copel.) Copel.	1500-1800 m	LMF	Borneo endemic
31. G. caespitosa Blume	1800 m	LMF	Sumatra to New Guinea
32. G. clemensiae (Copel.) Parris	3400-4000 m	UMF SA	Borneo to New Guinea
33. G. congener Blume	1100-2500 m	LMF	SE Asia to Philippines
34. G. dolichosora (Copel.) Copel.	1100-3000 m	LMF UMF	Borneo to New Guinea
35. G. friderici-et-pauli (H.Christ) Copel.	2000-2700 m	LMF UMF	Borneo, Sulawesi
36. G. graniticola Parris ined.	3300-3400 m	UMF	Mount Kinabalu endemic
37. G. havilandii (Baker) Copel.	1500-3200 m	LMF UMF	Mount Kinabalu endemic
38. G. holttumii Copel.	1700-2900 m	LMF UMF	Pen. Malaysia to Sulawesi
39. G. impressa Copel.	1200 m	LMF	Sumatra to New Guinea
40. G. intromissa (H.Christ) Parris	1400-2400 m	LMF	Taiwan to New Guinea
41. G. jagoriana (Mett. ex Kuhn) Tagawa	1400-2600 m	LMF UMF	SE Asia to Solomon Is.
42. G. kinabaluensis (Copel.) Copel.	1800-4000 m	LMF UMF SA	Mount Kinabalu endemic
43. G. knutsfordiana (Baker) Copel.	1500-2700 m	LMF UMF	Peninsular Malaysia to Fiji
44. G. locellata (Baker) Copel.	3200-3700 m	UMF SA	Sumatra to New Guinea
45. G. mollis Parris ined.	1400-1500 m	LMF	Borneo to Moluccas
46. G. muscicola Parris ined.	3400 m	UMF	Mount Kinabalu endemic
47. G. nubicola Parris ined.	3000-3200 m	UMF	Mount Kinabalu endemic
48. G. oblanceolata (Baker) Copel.	1200 m	LMF	Sumatra to Solomon Is.
49. G. padangensis (Baker) Copel.	3400 m	UMF	Sumatra to New Guinea
50. G. pilosiuscula Blume	1600-2500 m	LMF	Sumatra to Philippines
51. G. ramicola Parris ined.	1500-2600 m	LMF	Mount Kinabalu endemic
52. G. reinwardtii Blume	1100-1800 m	LMF	Sri Lanka to Solomon Is.
53. G. reinwardtioides Copel.	1200-2300 m	LMF	Borneo endemic

54. G. scabristipes (Baker) Copel.	1800-3000 m	LMF UMF	Sumatra to Vanuatu
55. G. sumatrana (Baker) Copel.	1500-3000 m	LMF UMF	Sumatra to New Guinea
56. G. ultramaficola Parris ined.	2400-3000 m	LMF UMF	Mount Kinabalu endemic
57. Prosaptia alata (Blume) H.Christ	800 m	HF	S India to Samoa
58. P. barathrophylla (Baker) M.G.Price	1200-1500 m	LMF	SE Asia to Philippines
59. P. borneensis Parris ined.	2100 m	LMF	Borneo endemic
60. P. celebica (Blume) Tagawa & K.Iwats.	1500-2100 m	LMF	Thailand to New Guinea
61. P. contigua (G.Forst.) C.Presl	1200-2900 m	LMF UMF	S India to Marquesas Is.
62. P. davalliacea (F.Muell. & Baker) Copel.	2900-3800 m	UMF SA	Pen. Malaysia to New Guinea
63. P. multicaudata (Copel.) Parris	1500-2100 m	LMF	Borneo to New Guinea
64. P. obliquata (Blume) Mett.	1500-1800 m	LMF	S India to New Guinea
65. P. venulosa (Blume ex Kunze) M.G.Price	2500-2900 m	LMF UMF	Java to New Guinea
66. Scleroglossum debile (Kuhn) Alderw.	1800-2600 m	UMF	Pen. Malaysia to New Guinea
67. S. gracillimum Parris ined.	1000 m	HF	Borneo endemic
68. S. pusillum (Blume) Alderw.	1500-3200 m	LMF UMF	Thailand to Solomon Is.
69. S. sulcatum (Kuhn) Alderw.	1500-3000 m	LMF UMF	Sri Lanka to Marquesas
70. Themelium curtisii (Baker) Parris	1400-2400 m	LMF	Sumatra, Borneo
71. T. fasciatum (Blume) Parris	2700-3400 m	UMF	Sumatra to New Guinea
72. T. halconense (Copel.) Parris	2100 m	LMF	Borneo, Philippines
73. T. taxodioides (Baker) Parris	2300-3000 m	LMF UMF	Borneo to New Guinea
74. X. hieronymusii (C.Chr.) Holttum	1200-1700 m	LMF	Thailand to Borneo
75. X. nudicarpa (Zamora & Co) Parris	2700-2900 m	UMF	Borneo, Philippines
76. X. subpinnatifida (Blume) Copel.	1500-2200 m	LMF	Pen. Malaysia to New Guinea

HF, hill forest (800-1200m). LMF, lower montane forest (1200-2600m). UMF, upper montane forest (2600-3500m). SA, subalpine communities (3500-3800m).

Table 4. Grammitidaceae of Gunung Mulu.

Species	Altitude	Vegetation	Distribution
1. Acrosorus friderici-et-pauli (H.Christ) Copel	1200-1800 m	LMF	SE Asia to Moluccas
2. A. streptophyllus (Baker) Copel.	1500-1800 m	LMF	Thailand to Philippines
3. Calymmodon borneensis Parris ined	1400-1700 m	LMF	Borneo endemic
4. C. conduplicatus (Brause) Copel.	1800 m	LMF	Borneo to New Guinea
5. C. cucullatus (Nees & Blume) C.Presl	1900 m	UMF	Pen. Malaysia to Solomon Is.
6. C. gracilis (Fée) Copel.	900-2000 m	LMF UMF	SE Asia to New Guinea
7. C. luerssenianus (Domin) Copel	1700-1800 m	LMF	SE Asia to Solomon Is.
8. C. pectinatus Parris ined.	1200-1800 m	LMF	Java to New Guinea
9. C. reconditus Parris ined.	2000-2300 m	UMF	Borneo to New Guinea
10. Chrysogrammitis musgraviana (Baker) Parris	1200-1800 m	LMF	SE Asia to Vanuatu
11. Ctenopteris blechnoides (Grev.) W.H.Wagner & Grether	200-1200 m	LF LMFS.	India to Society Is.
12. C. brevivenosa (Alderw.) Holttum	1300-2000 m	LMF UMF	Thailand to Vanuatu
13. C. brooksiae (Alderw.) Parris	400 m	LF	Sumatra, Borneo
14. C. mollicoma (Nees & Blume) Kunze	2100-2300 m	UMF	SE Asia to New Guinea
15. C. nutans (Blume) J.Sm.	2300 m	UMF	Pen. Malaysia to New Guinea
16. C. subminuta (Alderw.) Holttum	1700 m	LMF	Sumatra to Borneo
17. Grammitis adspersa (Blume) Blume	1000-1800 m	LMF	SE Asia to Fiji
18. G. bongoensis (Copel.) Copel.	900-1500 m	LMF	Borneo endemic
19. G. friderici-et-pauli (H.Christ) Copel.	1700 m	LMF	Borneo, Sulawesi
20. G. impressa Copel.	1200 m	LMF	Sumatra to New Guinea
21. G. jagoriana (Mett. ex Kuhn) Tagawa	1600 m	LMF	SE Asia to Solomon Is.

22. G. knutsfordiana (Baker) Copel.	2000 m	UMF	Peninsular Malaysia to Fiji
23. G. oblanceolata (Baker) Copel.	1000-1200 m	LMF	Sumatra to Solomon Is.
24. G. padangensis (Baker) Copel.	2300 m	UMF	Sumatra to New Guinea
25. G. pilosiuscula Blume	2000 m	UMF	Sumatra to Philippines
26. G. reinwardtii Blume	1700 m	LMF	Sri Lanka to Solomon Is.
27. G. reinwardtioides Copel.	1400-2000 m	LMF UMF	Borneo endemic
28. G. setosa Blume	1800-2000 m	LMF UMF	Sumatra to Sulawesi
29. G. sumatrana (Baker) Copel.	2000 m	UMF	Sumatra to New Guinea
30. G. vittariifolia (C.Chr.) Parris	200 m	LF	Pen. Malaysia to Borneo
31. Prosaptia alata (Blume) H.Christ	100-1200 m	LF LMF	S India to Samoa
32. P. barathrophylla (Baker) M.G.Price	600-800 m	LF LMF	SE Asia to Philippines
33. P. borneensis Parris ined.	2300 m	UMF	Borneo endemic
34. P. celebica (Blume) Tagawa & K.Iwats.	1800-2200 m	LMF UMF	Thailand to New Guinea
35. P. contigua (G.Forst.) C.Presl	500-1800 m	LF LMF	S India to Marquesas Is.
36. Scleroglossum crassifolium (Baker) C.Chr.	900-1600 m	LMF	Borneo endemic
37. S. gracillimum Parris ined.	1000-1200 m	LMF	Borneo endemic
38. S. pusillum (Blume) Alderw.	1600-2400 m	LMF UMF	Thailand to Solomon Is.
39. S. sulcatum (Kuhn) Alderw.	200-1800 m	LF LMF	Sri Lanka to Marquesas
40. Themelium halconense (Copel.) Parris	1800 m	LMF	Borneo, Philippines
41. T. sarawakense (Parris) Parris	1500 m	LMF	Borneo endemic
42. Xiphopteris alternidens (Ces.) Copel.	600 m	LF	Pen. Malaysia to Borneo
43. X. hieronymusii (C.Chr.) Holttum	400-1800 m	LF LMF	Thailand to Borneo

LF, lowland rainforest (100-800m). LMF, lower montane forest (800-1900m). UMF, upper montane forest (1600-2300m).

Table 4. Grammitidaceae of Gunung Mulu.

Species	Altitude	Vegetation	Distribution
1. Acrosorus friderici-et-pauli (H.Christ) Copel	1200-1800 m	LMF	SE Asia to Moluccas
2. A. streptophyllus (Baker) Copel.	1500-1800 m	LMF	Thailand to Philippines
3. Calymmodon borneensis Parris ined	1400-1700 m	LMF	Borneo endemic
4. C. conduplicatus (Brause) Copel.	1800 m	LMF	Borneo to New Guinea
5. C. cucullatus (Nees & Blume) C.Presl	1900 m	UMF	Pen. Malaysia to Solomon Is.
6. C. gracilis (Fée) Copel.	900-2000 m	LMF UMF	SE Asia to New Guinea
7. C. luerssenianus (Domin) Copel	1700-1800 m	LMF	SE Asia to Solomon Is.
8. C. pectinatus Parris ined.	1200-1800 m	LMF	Java to New Guinea
9. C. reconditus Parris ined.	2000-2300 m	UMF	Borneo to New Guinea
10. Chrysogrammitis musgraviana (Baker) Parris	1200-1800 m	LMF	SE Asia to Vanuatu
11. Ctenopteris blechnoides (Grev.) W.H.Wagner & Grether	200-1200 m	LF LMFS.	India to Society Is.
12. C. brevivenosa (Alderw.) Holttum	1300-2000 m	LMF UMF	Thailand to Vanuatu
13. C. brooksiae (Alderw.) Parris	400 m	LF	Sumatra, Borneo
14. C. mollicoma (Nees & Blume) Kunze	2100-2300 m	UMF	SE Asia to New Guinea
15. C. nutans (Blume) J.Sm.	2300 m	UMF	Pen. Malaysia to New Guinea
16. C. subminuta (Alderw.) Holttum	1700 m	LMF	Sumatra to Borneo
17. Grammitis adspersa (Blume) Blume	1000-1800 m	LMF	SE Asia to Fiji
18. G. bongoensis (Copel.) Copel.	900-1500 m	LMF	Borneo endemic
19. G. friderici-et-pauli (H.Christ) Copel.	1700 m	LMF	Borneo, Sulawesi
20. G. impressa Copel.	1200 m	LMF	Sumatra to New Guinea
21. G. jagoriana (Mett. ex Kuhn) Tagawa	1600 m	LMF	SE Asia to Solomon Is.

22. G. knutsfordiana (Baker) Copel.	2000 m	UMF	Peninsular Malaysia to Fiji
23. G. oblanceolata (Baker) Copel.	1000-1200 m	LMF	Sumatra to Solomon Is.
24. G. padangensis (Baker) Copel.	2300 m	UMF	Sumatra to New Guinea
25. G. pilosiuscula Blume	2000 m	UMF	Sumatra to Philippines
26. G. reinwardtii Blume	1700 m	LMF	Sri Lanka to Solomon Is.
27. G. reinwardtioides Copel.	1400-2000 m	LMF UMF	Borneo endemic
28. G. setosa Blume	1800-2000 m	LMF UMF	Sumatra to Sulawesi
29. G. sumatrana (Baker) Copel.	2000 m	UMF	Sumatra to New Guinea
30. G. vittariifolia (C.Chr.) Parris	200 m	LF	Pen. Malaysia to Borneo
31. Prosaptia alata (Blume) H.Christ	100-1200 m	LF LMF	S India to Samoa
32. P. barathrophylla (Baker) M.G.Price	600-800 m	LF LMF	SE Asia to Philippines
33. P. borneensis Parris ined.	2300 m	UMF	Borneo endemic
34. P. celebica (Blume) Tagawa & K.Iwats.	1800-2200 m	LMF UMF	Thailand to New Guinea
35. P. contigua (G.Forst.) C.Presl	500-1800 m	LF LMF	S India to Marquesas Is.
36. Scleroglossum crassifolium (Baker) C.Chr.	900-1600 m	LMF	Borneo endemic
37. S. gracillimum Parris ined.	1000-1200 m	LMF	Borneo endemic
38. S. pusillum (Blume) Alderw.	1600-2400 m	LMF UMF	Thailand to Solomon Is.
39. S. sulcatum (Kuhn) Alderw.	200-1800 m	LF LMF	Sri Lanka to Marquesas
40. Themelium halconense (Copel.) Parris	1800 m	LMF	Borneo, Philippines
41. T. sarawakense (Parris) Parris	1500 m	LMF	Borneo endemic
42. Xiphopteris alternidens (Ces.) Copel.	600 m	LF	Pen. Malaysia to Borneo
43. X. hieronymusii (C.Chr.) Holttum	400-1800 m	LF LMF	Thailand to Borneo

LF, lowland rainforest (100-800m). LMF, lower montane forest (800-1900m). UMF, upper montane forest (1600-2300m).

Table 5. Geographic Distribution of Grammitidaceae of Mount Jaya, Murkele Ridge, Mount Kinabalu and Gunung Mulu

Geographic distribution	Species no. and percentage of total species Mount Jaya	Murkele Ridge	Mt Kinabalu	Gunung Mulu
1. Widespread beyond Malesia, to Polynesia and/or Sri Lanka	4, 70%	5, 90%	8, 11%	5, 12%
2. Malesia-wide or slightly beyond, or at least across Zollinger's line	24, 43%	31, 56%	44, 58%	22, 51%
3. E Malesia (MJ, MR) or W Malesia (MK, GM)	4, 70%	9, 16%	10, 13%	9, 21%
4. Country endemic	20, 36%	1, 20%	5, 70%	7, 16%
5. Locality endemic	4, 70%	9, 16%	9, 12%	0, 00%
Species total	56	55	76	43

DISCUSSION

Compared with Murkele Ridge, Mount Kinabalu and Gunung Mulu, Mount Jaya has many more country endemics. This reflects the explosive speciation of Grammitidaceae in New Guinea (together with many other groups of plants) and their distribution along the central ranges of the island. The wide distribution of species along the central ranges of New Guinea is probably also an explanation for the low number of endemic species compared with Mount Kinabalu and Murkele Ridge. While Mount Jaya is the highest peak in a series of high altitude peaks on the ranges that form the backbone of New Guinea, Murkele Ridge and Mount Kinabalu are isolated from other areas at high altitudes. Mount Jaya and Gunung Mulu have fewer species that are widespread in Malesia and beyond than do Murkele Ridge and Mount Kinabalu. Gunung Mulu, being relatively low altitude, does not have the array of habitats or even comparable areas of the same habitats as do the higher Murkele Ridge and Mount Kinabalu. The reason for Mount Jaya having fewer of the widespread species is less obvious. In the discussion of Murkele Ridge (see above), seven widespread species are mentioned that are absent from Mount Jaya, but present in New Guinea and thus to be expected. Another two species that occur on Mount Kinabalu and are disjunct with Papua New Guinea are also expected on Mount Jaya. They are *Calymmodon atrichus* and *Grammitis clemensiae*.

There is a group of 10 grammitid species that have been collected on all of the four montane Malesian localities documented here: they are *Calymmodon cucullatus*, *Chrysogrammitis musgraviana*, *Ctenopteris blechnoides*, *C. nutans*, *Grammitis knutsfordiana*, *G. padangensis*, *G. sumatrana*, *Prosaptia contigua*, *Scleroglossum pusillum* and *S. sulcatum*. Two other widespread high altitude subalpine species are not found on Gunung Mulu (2400 m alt.) because it is too low: *Grammitis locellata* (2800-3800 m) and *Prosaptia davalliacea* (2800-3800 m). Another group of species, *Calymmodon clavifer*, *Ctenopteris denticulata* ,*C. millefolia*, *C. subsecundodissecta*, *Grammitis dolichosora*, *G. intromissa*, *G. scabristipes*, *Prosaptia obliquata*, *P. vemulosa* and *Xiphopteris subpinnatifida* occur on Mount Jaya, Murkele Ridge and Mount Kinabalu within the altitudinal range of Gunung Mulu and may be expected there. The widespread *Grammitis reinwardtii* is absent from Mount Jaya, but occurs in the other three localities. The species that are absent from Gunung Mulu and from Mount Jaya, together with the 10 listed above, form a core of 23 grammitid species that are widespread and common throughout Malesia. Examination of herbarium collections during preparation of the account of Grammitidaceae for Flora Malesiana has provided much detailed data on species distribution that has been collated for over 500 localities. The core group of 23 grammitid species is well-represented in the following localities, each of which has 20 or more species of Grammitidaceae. The altitude range over which Grammitidaceae have been collected and the number of species currently known is given for each locality. Peninsular Malaysia: Cameron Highlands, 1400-2000 m, 23 species; Gunung Tahan, 600-2200 m, 21 species; Sumatra, Gunung Kerinci, 300-3800 m, 22 species; Java, Gunung Gede, 1200-3000 m, 39 species; Sulawesi, Mount Roroka Timbu, 1200-2400 m, 25 species; Philippines, Mount Apo, 1000-3000 m, 25 species; Papua, Mount Trikora, 2800-4200 m, 36 species, Idenberg River, 700-2200 m, 22 species; Papua New Guinea, Aseki, 1300-1800 m, 20 species, Ekuti Range at Watut-Aseki Divide, 2000-2100 m, 22 species, Mount Giluwe, 2100-4100 m, 38 species, Mount Hagen, 2400-4000 m, 34 species, Rawlinson Range, 1500-4000 m, 33 species, Saruwaged Range, 1200-4000 m, 40 species, Star Mountains, 1400-4000 m, 24 species, Mount Suckling, 400-3700 m, 20 species, Mount Wilhelm, 2700-4500 m, 26

species.

The identification of pteridophytes below the subalpine and alpine areas of Mount Jaya is not yet complete (R.J. Johns pers. comm.), so a complete evaluation of the relationships of the pteridophyte flora is not yet possible. Ridley (1916) records a number of pteridophytes from Mount Jaya, however, and this is sufficient to establish that there is a core of widespread pteridophytes in families other than Grammitidaceae that are also present on Mount Kinabalu (Parris *et al.*, 1992), Murkele Ridge (Parris, 1993) and Gunung Mulu (Parris, unpublished). They include *Asplenium tenerum* G. Forst., *Diplazium cordifolium* Blume, *Lindsaea rigida* J. Sm. (Kato, 1992), *Lycopodiella cernua* (L.) Pic. Serm., *Ophioglossum pendulum* L. (Kato, 1989b), *Selliguea enervis* (Cav.) Ching and *Trichomanes pallidum* Blume.

CONCLUSIONS

Mount Jaya has some unique features compared with the other Malesian mountains considered here: the presence of a rich grammitid flora in the heath forests between 200 and 600 m alt. is unexpected, and there is a good representation of widespread New Guinea endemic Grammitidaceae. The absence of high altitude endemics in the family is surprising, given that several other high New Guinea mountains have one or more endemic species. Mount Jaya is much less species-rich than Mount Kinabalu, and this may be explained at least in part by the much longer history of collecting on the latter and the paucity of collections from the largely inaccessible upper montane forest of the former. Compared with Mount Jaya, the Murkele Ridge, 2000 m lower, supports a rich flora of Grammitidaceae, but the reason for this is not evident.

Zollinger's line does not present an insuperable barrier to the distribution of Grammitidaceae, as 59 (45 %) of the 130 species listed in Tables 1 to 4 occur on both sides of it.

The concept of a core Malesian-wide pteridophyte flora present in all suitable areas has not been suggested previously, but there is ample evidence for it in 23 species of Grammitidaceae and numerous species in other pteridophyte families.

ACKNOWLEDGEMENTS

I wish to thank Robert Johns and Peter Edwards (K) for organising the loans of Kew specimens, Alison Paul (BM) for seeking out Kloss' collections, the Keepers of BM and K for the loan of material and Ewen Cameron (AK) for facilitating the loans.

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MORPHOGENETIC EVENTS IN THE *CERATOPTERIS RICHARDII* (PARKERIACEAE: PTERIDOPHYTA) SHOOT APEX

M. ROMANOVA[1] & J. JERNSTEDT[2]

Department of Agronomy and Range Science, University of California, David, CA 95616, USA. (Email: [1]maromanova@ucdavis.edu; [2]jjernstedt@davis.edu)

Keywords: Shoot apex meristem, shoot apical cell, leaf apical cell, leaf primordium, plasmodesmata, morphogenesis, development, dictyostele, protostele

The discovery of developmentally important genes, combined with remarkably regular cell division patterns, has made the *Ceratopteris richardii* sporophyte an advantageous system for developmental studies. Here we report results of an investigation of the ontogenetic changes in shoot apical meristem (SAM) structure associated with leaf initiation and histogensis in *C. richardii*. As described for a number of other ferns, the shoot apical cell (AC) and leaf apical cell (LAC) of the first leaf of *C. richardii* embryos appear simultaneously; all subsequent sporophyte leaves originate from the SAM. An LAC originates in every immediate derivative of the tetrahedral AC. After this segment is displaced from the AC by two, more recent derivatives, it undergoes two anticlinal divisions and one transverse division, setting up the LAC. The pattern of LAC origin does not change during sporophyte ontogeny, but the rhythm of leaf development does. For the first leaves of a young sporophyte, the subsequent division of the AC is correlated with further proliferation of cells of the incipient leaf primordium (LP), and the AC does not undergo further divisions until the LP is established. Development of the first 6-9 leaves is followed by a developmental pause of 12-20 days, during which the shoot apex changes its structure and morphogenetic pattern. LPs are arrested at the 4- or 5-cell stage until displaced some distance from the AC, which continues to segment and creates an increasing "pool" of early stage LPs. This results in an elongated shape for the shoot apex. These changes are correlated with changes in the shoot vascular system. A protostele is found in the young sporophytes with simple leaves developing without pause; each leaf has a unibundle leaf trace (LT). Dictyosteles occur in older sporophytes bearing compound leaves; these leaves start to develop when separated from the AC by a number of incipient LPs, and have 2-5 bundles per LT. Procambium differentiates simultaneously with LP development; no signs of vascular differentiation are observed in either the juvenile or the adult shoot apex. Ontogenetic changes in stelar type might be explained by the loss of meristem identity and competence to differentiate into procambium by the central cells of the apex. This is in agreement with Sano *et al.* (unpublished observation) that KNOX class I genes are expressed in the AC and procambium of *C. richardii* adult sporophytes (but not in the other cells of the elongated apex). Because plasmodesmata (PD) provide selective routes for signaling within the shoot apex, we examined PD architecture and distribution in the *C. richardii* SAM. All PD in the *C. richardii* SAM are primary. PD density in the AC and its immediate derivatives does not change significantly in sporophyte ontogeny but is about ten-fold higher than reported for dicot SAMs. High PD density and the resulting intercellular connectedness may compensate for the lack of ability to form secondary PD. Only the AC and its two immediate derivatives, the latter being constantly displaced, are interpreted to be undifferentiated in the *C. richardii* SAM.

REPRODUCTIVE STRATEGIES AND POPULATION STRUCTURE IN THE ENDANGERED PTERIDOPHYTE *TRICHOMANES SPECIOSUM* (HYMENOPHYLLACEAE: PTERIDOPHYTA)

F.J. RUMSEY[1], J.A. BARRETT[2*], M. GIBBY[3], S.J. RUSSELL[1] & J.C. VOGEL[1]

[1]Dept. of Botany, The Natural History Museum, Cromwell Road, London, UK.
[2]Dept. of Genetics, University of Cambridge, Cambridge, UK;
[3]Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, UK.
(Email: F.Rumsey@nhm.ac.uk)

Keywords: Glacial refugia, gametophyte, historical biogeography, dispersal, filmy-fern.

ABSTRACT

Trichomanes speciosum Willd. (Hymenophyllaceae) is unique amongst European ferns in that the gametophyte generation can survive indefinitely in the absence of the sporophyte, propagate vegetatively and disperse locally. Reproductive success, both in terms of spore production and sporophytic recruitment currently vary widely across the species' broad, disjunct range, declining from south to north and west to east. Reproductive success would appear to be controlled largely by climatic factors, although genetic components also must be considered. Detailed study of populations throughout the species' range, over a 15 year period, have led to a greater understanding of growth rates, powers of dispersal and the reproductive strategies currently operating. Using this knowledge, the extent and pattern of genetic variation regionally and locally, i.e within sites, can be used to infer the routes and mechanisms of colonisation and subsequent reproductive history.

Many sites for this species have been considered as glacial refugia, i.e., supporting relictual populations through cycles of glaciation throughout the Tertiary. The validity of these claims is tested using molecular and other data.

INTRODUCTION

Trichomanes speciosum Willd. (syn. *Vandenboschia speciosa* (Willd.) Kunkel), the Killarney Fern, is the sole native European representative of the genus *Trichomanes sensu lato* (Tutin *et al.*, 1993) and the largest of the region's filmy-ferns (Hymenophyllaceae). It has been considered one of the continent's most vulnerable plant species, threatened both by habitat destruction and long the victim of over-collection, and has been accorded legal protection throughout its range under the Bern Convention (Anon, 1979) and E.C. Habitats Directive (Anon, 1992).

Trichomanes speciosum is unique amongst European ferns in that its gametophytic generation is perennial, gemmiferous and capable of persisting and dispersing in the absence of a sporophyte. This 'gametophytic independence' is apparently a very rare condition amongst homosporous ferns, and known in three families, all widespread as epiphytes in tropical regions: the Vittariaceae, the Grammitidaceae, and the Hymenophyllaceae. However, gametophytic independence is apparently only well developed in those rare species found at the temperate extremes of these families'

ranges (Rumsey & Sheffield, 1996).

Independent gametophytes of a *Trichomanes* species were first tentatively identified from eastern North America by Wagner & Evers (1963) and confirmed by Farrar (1967, 1985, 1992) who identified a distinct taxon, *T. intricatum* Farrar (Farrar, 1992) represented solely by gametophyte populations.This taxon was found to exist far to the north of the line of the last glacial maximum, indicating it clearly had the ability to disperse over some distance, even if sporophytes and hence spores were currently not produced. The other widespread North American species of *Trichomanes* have been found as gametophyte populations but always in close proximity to sites in which sporophytes are present (Farrar, 1993). The situation in Europe falls between these extremes and differs in scale, in that both generations of *T. speciosum* are known, but the gametophyte has an extensive range (hundreds of kilometres) beyond that of the sporophyte.

Reproductive Potential and Strategies

The sporophyte of *T. speciosum* has a long-running, branching rhizome, at intervals bearing fronds which are functional for 4 or more years, and may persist for longer. Rhizome growth rates are heavily dependant on the plant's nutrient status and climatic environment but main axes may elongate by over 30 cm per annum, although usually by much less. Suppressed side branches borne in the sporophyll axils allow for steady patch formation should the leader not find suitable habitat and die. This growth form allows a guerrilla-type growth strategy similar to that employed by species of *Lycopodium* to exploit patchy environments (Callaghan *et al.*,1986). Specialised mechanisms of vegetative propagation are absent (viviparous plantlets have been recorded twice in cultivated material over two centuries of observation (Druery,1910; Ensoll, pers comm.)). Rhizome fragmentation, dislodgement and re-growth are likely to be infrequent but significant events. Extensive, intricate and usually dense patches form with time. Within these it is generally impossible to determine the number of individuals present without recourse to molecular techniques. Individual clones covering several hundred square metres have been recorded by the authors in the Azores, obviously indicative of considerable antiquity. However, colony size is not necessarily an accurate indication of age. Several British colonies known for over a century are very restricted in size, their maximal extent presumably determined by the extent of the micro-features that they grow in.

Unlike many European ferns *Trichomanes speciosum* is not fertile annually once mature. Indeed Ratcliffe *et al.*, (1993) reported that the majority of British sporophytes had never been seen to be fertile. Detailed investigation of fertility is difficult and in many cases not desirable because of the nature of the sites occupied. However, during the last decade four Welsh and two English sporophytes known to the authors have at least attempted to produce spores. Involucres have formed but the receptacular bristle upon which the sporangia are spirally borne has, in at least two of the sites, not extended and no spores have formed as a consequence. This receptacular bristle structure has a basal meristem and presumably continues to elongate and produce new sporangia until a certain trigger, perhaps desiccation causing sporangial dehiscence, causes it to cease. Its failure to develop in marginal British sites may have climatic cause, such as exposure to cold. This and the factors determining the onset of fertility are almost certainly complex and have not been established for *T. speciosum*. Anecdotal evidence would seem to suggest that sporophytes in extreme shade are less regularly fertile and,

as most plants at the more northern and marginal extremes of the species range are progressively restricted to more sheltered and hence usually darker microsites, this alone may account for the reduction in northern fertility. Considerable variation exists in the degree of fertility, i.e. the number of involucres produced – dictated by frond stature and dissection, and the number of sporangia produced per involucre, as outlined above. Sporophytes in northern and more easterly British sites are invariably small and relatively poorly dissected, reducing sporing potential. Calculations based on observation of the number of fertile fronds known in all British populations for one year, an estimated mean number of involucres per frond and numbers of sporangia per involucre, suggested that the total British spore production per decade would be considerably less than that produced by a single healthy adult *Athyrium filix-femina* in one year (Rumsey, 1994) ! The species is thus likely to be a poor coloniser by spore or vegetative means.

Sporophyte recruitment parallels the pattern of spore production in that there is a marked reduction in the production of sporophytes northwards, i.e. into northern France and the British Isles and even more markedly, eastwards into continental Europe. Thus within the wetter portions of Macaronesia the species functions as a "normal" pteridophyte, completing its life cycle from spore to spore, whereas elsewhere the cycle progressively breaks down, until over much of the species extensive distribution in northern and continental Europe the gametophyte is effectively functionally independent. Immature sporophytes have rarely been noted within the British Isles and show high levels of mortality (Rumsey, 1994), although recent years have perhaps shown an increased incidence in their production ("Sentinel", 2003; Rumsey, unpubl.) which may be a reflection of the run of warm but wet summers and milder winters experienced in the British Isles. Immature sporophytes have also been reported in central Europe, eg. Rasbach *et al.*, 1994 which indicates that gametangial production and normal function are occurring in at least some "independent" gametophytic clones. Given a potentially indefinite gametophytic lifespan the probability must be that sporophytes would form, although perhaps extremely infrequently, in the vast majority of populations.

Sporophytic production and recruitment almost certainly is predominantly a reflection of the rate and extent of gametangial production. The archegoniophore is a comparatively massive, differentiated, multicellular structure unlike the simple irregular branching filamentous structure it is borne on. The processes triggering its initiation are unknown but rates of cell growth and light/nutrient availability might be implicated. The smaller antheridia are more regularly produced and may persist in a non-dehisced state for many months. Rumsey & Sheffield (1996) summarised knowledge on the *in situ* and *ex situ* production of gametangia by different British gametophyte clones over a 5 year period. They identified consistent sterility, or super-fertility, of some clones, even when sub-divided and grown apart under similar but not rigorously controlled growth conditions, suggesting a significant genetic component to gametangial production, but with no clear geographical, ecological or discernible historical basis. Locally this may complicate considerations of the effect of climatic and other external factors on gametangial production but broad regional differences, which are reflected in sporophyte recruitment, are still apparent.

Understanding the Current Distribution- Refugia or Recent Colonisation?

First detected as recently as 1989 (Rumsey *et al.*, 1990; 1991), subsequent survey has

revealed the gametophyte to be widespread but extremely localised within the British Isles, significantly occurring in many areas from which the sporophyte had never been reported (Rumsey *et al.*, 1998). Similarly, as the distinctive habit and habitat of the gametophyte became known, discoveries across northern continental Europe rapidly followed, e.g. Vogel *et al.*, 1993; Rasbach *et al.*, 1994; Bennert et al, 1994; Bujnoch & Kottke, 1994: Kirsch & Bennnert, 1996; Horn & Elsner, 1997; Huck, 1997; Reichling, 1997; Boudrie, 2001; Krippel, 2001, Loriot *et al.*, 2002, Kottke, 2003, etc.

Initial reports were from deeply dissected sandstone massifs, such as the Petite Suisse of Luxembourg, the northern Vosges and the Elbsandsteingebirge, all areas noted for the occurrence of other rare, disjunct 'Atlantic' taxa (*sensu* Ratcliffe, 1968) but particularly the filmy-fern *Hymenophyllum tunbrigense* (L.) Sm. (Richards & Evans, 1972). In these disjunct areas *H. tunbrigense* has been considered to be a Tertiary relict (Drude, 1902; Klein, 1926). Subsequent examination has revealed the gametophyte of *Trichomanes speciosum* to be more widely distributed and in less "exceptional" landforms and habitats in intervening regions in western and Central Europe, such that the recorded distribution of the species is now much less discontinuous and more extensive than previously realised. This raises interesting questions as to when this broader gametophyte distribution was achieved and from where?

The broad continental and northern-European distribution of *Trichomanes speciosum* may have been achieved as a result of a wave of post-glacial migration from southern and western refugia, or conversely from limited diffusion from a range of more northerly peri-glacial refugia, or indeed result from an amalgam of both. Sites containing gametophytes alone may thus represent recent arrivals, or the tenacious survivors of a species uniquely suited to coping with a sub-optimal climate. Sadly, few relevant sub-fossil or palynological finds are known, or are realistically to be expected. Comparison with the distribution of other taxa can be informative, but elucidation of the species quarternary history is largely reliant on molecular studies of the pattern, extent and structure of genetic variation throughout the species range. Knowledge of the comparative reproductive and dispersive capabilities of the different generations can then be used to infer whether sporophytes were likely to be present historically in areas from which they are now unknown.

Generally our expectation must be that sites which have been suitable for the peri-glacial survival of a particular species are likely to have allowed the survival of a suite of taxa, and that this community, or many of its distinctive components may well recur in other disjunct refugial sites. The peculiar biology of *Trichomanes speciosum* and its ability to grow in conditions that are not conducive to the survival of all other vascular plants may, however, mean that it is a special case.

We also expect refugial sites to support greater genetic diversity than those which have been recently colonised. A potential confounding factor is that of severe bottlenecking – low or no diversity may result from loss over time/genetic drift, as well as by founder effects. We must also consider that an efficiently vegetatively-reproducing organism of narrow ecological amplitude might effectively block niches and thus prevent the arrival of other individuals ("the first in wins"). Variation may then be reliant on the rates of mutation in the various ramets, although these would be expected to accrue with time, meeting our original expectation. Ancient refugial sites, if isolated, might be expected to show private variation, i.e. unique to them, although post-glacial dispersion, if efficient, will obscure such patterns.

Refugia or Not?

Several disjunct areas are now known to support very small populations of *Trichomanes speciosum,* many of which have been discovered comparatively recently. Within these the relative proportion of sporophytes vs. gametophytes differs but many show comparably low levels of sporophytic presence and association of a suite of Atlantic species. Do they and their associated species show similar levels and patterns of genetic diversity and what can this reveal as to their history?

Southern Spain

Trichomanes speciosum was first discovered in Southern Spain by Richards (1934) and is now known from a very limited range of sierras leading inland from the coast near Algeciras, northwards to near Cortes de la Frontera (Rumsey & Vogel, 1998; Garrido Díaz & Hidalgo Maqueda, 1998). Currently nine populations are known to be extant, more than half (5) of which are thought to support fewer than 10 discrete sporophyte clumps each. Only one site (Sierra de Montecoche) currently contains gametophytes in the absence of sporophytes. The species main concentration is in the Sierra de Ojén and its westward continuation, the Sierra de Saladavieja. Here a total of approaching 200 distinct mature regularly fertile sporophytic clumps, closely associated with small localised areas of gametophyte and numerous juvenile sporophytes, occur in 12 distinct sub-populations by parallel small watercourses. High levels of mortality, with extreme reductions, at least in sporophyte populations, linked with the cycles of cork-oak harvesting and climatic variation, have been documented in the recent past (Molesworth-Allen, 1977).

Allozymic study of material from 3 sites: Sierra de Ojén (4 sub-populations), the Valle del Río de la Miel and the Sierra de Montecoche, indicates that each site had alleles not shared with the other sites (Table 1) and that the large Sierra de Ojén site contained at least 16 different multilocus phenotypes (MLPs), 10 of which were present in the largest sampled sub-population. The observed differences between closely adjacent watercourses may indicate low levels of gene-flow even over such restricted ranges but patterns indicate the likelihood of intergametophytic mating within these sub-populations, with the fern fully completing its life cycle and behaving in a "normal" pteridophytic fashion, unlike populations further north in its range.

These small populations co-exist with a limited range of Macaronesian bryophytes unknown elsewhere in Mainland Europe (Rumsey & Vogel, 1999) as well as other pteridophyte taxa, including *Culcita macrocarpa*, *Diplazium caudatum*, *Pteris incompleta* and previously *Dryopteris guanchica* – the latter suggesting a closest affinity with the Canarian flora. This floristic enclave, with fragmentary representation on the adjacent North African coast and into the Rif mountains, either represents the vestige of a once wider coastal African/Canarian/Iberian distribution fragmented by aridification and the increase of the Saharan desert area, or, and less likely, represents independent post-glacial (re-)colonisation by the many and varied Macaronesian floral elements. All potentially are highly dispersible given the small size of their diaspores.

Alpi Apuane, Italy

Trichomanes speciosum was found, new to the Italian flora, only as recently as 1976 (Ferrarini, 1977). Subsequently a total of five "populations" have been detected growing within the stream gorge of the Valle de Serra and its side valleys, close to the town of Serravezza (Marchetti, in Ferrarini *et al.*, 1986). Few discrete individual mature

Table 1. Distribution of multilocus phenotypes (MLPs) in southern Spanish *Trichomanes speciosum* populations (figures represent the number of apparently discrete individuals possessing that MLP).

Allozyme Phenotype				Site					
PGM	IDH	6-PGD	MDH	Miel	Ojén 1	Ojén 2	Ojén 3	Ojén 4	Monte -coche
A	A	A	A						2
A	A	A	B		5	9			
A	A	A	D		3			1	
A	A	A	E		3	1		2	
A	A	B	B		2	2	3	4	
A	A	B	D					4	
A	A	B	E			4			
A	A	B	F					1	
A	A	D	B					1	
A	B	A	E		4				
A	B	B	-					1	
B	A	A	B		26	1			
B	A	B	E		1				
B	A	B	F		1				
B	B	C	E		1				
B	C	A	A	1					

sporophytes are known but at least one is extensive and regularly highly fertile. The known sporophytes share a distinctive and apparently unique morphology.

Initial researches indicate a wider distribution of the gametophyte (Rumsey & Vogel, unpubl.), perhaps paralleling that of another disjunct Atlantic element, the filmy-fern *Hymenophyllum tunbrigense*, for which ca. 70 sites are known in the communes of Massa, Montignoso, Stazzema, Pietrasanta, as well as Serravezza (Pichi-Sermolli, 1936; Marchetti, 1992). Sporophytic recruitment has been observed in sites containing mature sporophytes but not in sites currently only known to support gametophyte populations.

Unfortunately only a limited range of material has been available for analysis. Both localities from which multiple samples have been taken support more than one MLP (3 & 5) with patterns consistent with the occurrence of intergametophytic mating.

Sporophytes are currently unknown in the most genetically diverse of these sites. One allele in the enzyme PGM has not to date been recovered in any other *Trichomanes speciosum* population throughout its global range.

All the evidence would thus tend to argue that this area must be considered refugial.

Southwest Scotland

In contrast to the Iberian and Italian sites this area was heavily glaciated and the species occurrence here must result from post-glacial (re-) colonization. It is thus instructive to compare the patterns of distribution and extent of genetic variation with the almost certainly refugial areas above and more equivocal areas.

Fewer than 20 discrete sporophyte plants have been detected in Scotland since its first discovery in 1863 (Babington, 1863) and less than half this number are known to be extant. Only one of these colonies has ever been seen to produce spores and most are, or were, very limited in size and extent. However, the gametophyte generation is widespread and may be locally abundant. Recent recruitment of sporophytes has been seen to occur both in sites containing mature sporophytes and also in at least one site were these were absent.

Genetic diversity of the species at this the northern-most limit of its distribution was studied by Rumsey *et al.*, (1999). 121 samples from 37 populations in 22 sites were examined and 7 allozyme MLPs were detected. Two of these MLPs covered large areas (>30 km in total extent), while the others were restricted to one, or rarely few, localities. No site was found to contain more than one MLP. Whether this is evidence for blocking of available niches by the first arrival, or merely a reflection of the extreme rarity of propagules of other MLPs arriving in occupied sites is unclear and may require experimental verification through deliberate introduction. The extent of MLPs was not correlated with presence /absence of sporophytes. Where they extend over many kilometres, in some cases on separate islands, the only credible means of dispersal is by spore. Where sporophytes are currently unknown such a distribution indicates their past presence, and a greater fertility than in the recorded past. Sporophytes may have occurred as long ago as in the sub-atlantic period, or during brief warm wet phases subsequently – such as we appear to be experiencing currently. Very broad distributions must indicate considerable age given the poor dispersal powers shown by both generations of this organism. It is tempting to speculate that geographical extent could be correlated with arrival time but many conflicting factors have also to be considered.

Communities in glaciated and un-glaciated areas share many rare and disjunct taxa and their presence alone is un-informative as to refugial status, but the population structure and genetic make-up of these taxa is much more revealing. Many of the Macaronesian bryophytic taxa show disjunctions to southwest Scotland, but the majority of these diocious species are represented by one sex alone in the British Isles, yet exist in mixed sex populations and fruit in southern (refugial?) areas. Such a pattern might be expected given extremely rare long-range post-glacial dispersal events to the north.

Central Europe

Rumsey *et al.*, (1998) examined allozymic diversity in 35 sites from the then easternmost known extent of the species distribution in the Elbsandsteingebirge on the Czech- German border, through Germany to the French border in the northern Vosges mountains. The extensive distribution of some MLPs, as in Scotland, indicated that

sporophytes almost certainly must have been present in the past. The majority of sites supported single MLPs ; however some sites in the pfälzerwald supported multiple MLPs, some of which are indicative of past inter-gametophytic mating and thus by inference sporophyte production. From the allozyme data alone Rumsey *et al.*, (1998) suggested that post-glacial spread was more likely but were unable to exclude the possibility that some at least of these locations may have acted as refugia for the species. The levels of intra-population variation, even though low, and the presence of unique simple banding patterns for two enzyme systems (ACON, 6-PGD), gave support to this notion but the proximity of glacial forelands to many of the current localities suggested survival was less likely (Vogel *et al.*, 1993). Subsequent work by Rumsey *et al.* (in prep.), sequencing of the chloroplast DNA haplotypes first reported by Rumsey *et al.* (1996) has provided additional evidence which would appear to strengthen the case for, at least limited, peri-glacial survival. Macaronesian island refugia show a major dichotomy between the Azores in the north, and Madeira and the Canaries to the south. Minor haplotype variants link some Canarian populations with those from southern Iberia, supporting the broad floristic links already known. Investigated areas of Europe on the western Atlantic seaboard from Brittany northwards show a mix of the haplotypic variants found in the southern refugial sites, although not an intimate one (i.e. sites contain single haplotypes in all cases). The overall picture created is in contrast with the usual pattern of Northern Purity – Southern Richness reported by Hewitt (1999) and others. Interestingly, central Europe is uniformly of the Azorean, believed to be ancestral, type, in spite of the fact that all of the nearest spore sources (Spain, Italy) are of the contrasting major haplotype. If the distribution were the result of post-glacial immigration one might expect a similar pattern to that shown in northwest Europe, with all of the refugia and particularly the most proximal to be involved. Unique minor variants also exist within central Europe, for example in Luxembourg, where they cover an extensive area indicative of a long period of occupation and/or past sporophyte presence. Extremely severe conditions in proximity to sites and the growth and reproductive strategies of *Trichomanes speciosum* may explain the lack of expected diversity in these putatively refugial areas.

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PTERIDOPHYTE DIVERSITY IN LUXEMBOURG

Y. KRIPPEL

Research associate of the Natural History Museum of Luxembourg
Rue de Rollingen, 18A; L - 7475 Schoos, Luxembourg
(Email: yves.krippel@mnhn.lu)

The Grand-Duchy of Luxembourg is internationally known for its small relictual population of Tunbridge filmy-fern (*Hymenophyllum tunbrigense* (L.) Sm.), first discovered here in 1821. In recent decades, however, ferns and allied plants - especially subspecies and hybrids - have often been neglected by botanists in Luxembourg, so that reliable data about distribution and status of pteridophyte species is often lacking. Over the last few years, the study of the pteridophytes of Luxembourg has been relaunched, and previous deficiencies in information are being reduced progressively.

Despite the small geographic area of Luxembourg (2586 km^2), the diversity of pteridophytes is remarkable. A great number of geological substrates, special geomorphological features with particular microclimatic conditions and a great variety of habitats, ranging from acidic to rather base-rich, have favoured the luxuriant development of a certain number of ferns and fern allies. Not less than 57 pteridophytes (species, subspecies, nothosubspecies and hybrids) are known for Luxembourg. Regrettably a certain number of species have not been observed in the recent decades and can be considered as extinct in wild. Fortunately new taxa have been discovered recently, such as *Trichomanes speciosum* Willd. (gametophytes), *Asplenium trichomanes* L. subsp. *pachyrachis* (Christ) Lovis & Reichstein, *Asplenium trichomanes* L. nothossp. *staufferi* Lovis & Reichstein, *Asplenium* x *murbekii* Dörfler and *Equisetum* x *litorale* Kühl. ex Rupr. At present the pteridophyte flora of Luxembourg includes five clubmosses, seven horsetails and 45 ferns. The Red List, based on the checklist of the pteridophytes of Luxembourg, applies the revised IUCN Red List categories (IUCN 2001) at a national level. Currently 14.7% of the taxa fall in the category Regionally Extinct (RE), 6.5% are Critically Endangered (CR), 6.5% Endangered (EN), 8.2% Vulnerable (VU) and 18% Extremely Rare (R). Only c. 40% of all pteridophyte taxa are considered not to be threatened (*) for Luxembourg.

Despite the recent discoveries of new taxa, the pteridophyte flora of Luxembourg has experienced a significant loss of species. This is predominantly due to habitat changes and resulting climatic variations (habitat destruction, deforestation, changes in drainage patterns etc.). Management plans for rare and endangered species may prevent further loss. For critical species and extremely threatened sites, however, it is advisable to envisage securing the collection through ex-situ conservation and storage of representative samples for future scientific purposes.

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SOME NOTES ON THE TAXONOMY, BIOGEOGRAPHY AND ECOLOGY OF *DANAEA* (MARATTIACEAE)

M.J.M. CHRISTENHUSZ[1] & H. TUOMISTO[2]

Department of Biology, University of Turku, FI-20014 Turku, Finland,
(Email: [1]maarten.christenhusz@utu.fi, [2]hanna.tuomisto@utu.fi)

Key words: Biogeography, *Danaea*, ecology, Marattiaceae, Neotropics, phylogeny, taxonomy.

ABSTRACT

The neotropical genus *Danaea* is in revision and some notes on the genus are presented here. We find that the genus can be divided into three subgroups, based on morphological characters of the rhizome, stipe articulation and pinna margin serration. The tree groups are discussed and some taxonomic issues are addressed. The occurrence of bipinnate *D. nodosa* is reported from Jamaica, and trifoliate specimens of *D. simplicifolia* are reported from French Guiana. The identities of *D. alata, D. jamaicensis, D. jenmanii, D. mazeana, D. media, D. nodosa, D. trifoliata* and *D. ulei* and their synonyms are discussed. Further studies on the phylogeny, taxonomy and ecology of *Danaea* are needed.

INTRODUCTION

The genus *Danaea* Sm. is one of the few genera of ferns confined to the Western Hemisphere. It has been repeatedly observed that species limits within the genus are poorly understood, and that the genus is in great need of monographic study (e.g., Morton, 1951, Kramer, 1978). De Vriese & Harting (1853) monographed the Marattiaceae but excluded *Danaea*, which was at the time, placed in a separate family: the Danaeaceae. Underwood (1902) revised the North American species, and the Ecuadorian species were recently revised by Tuomisto and Moran (2001), but many taxonomic problems remain. In the recent monograph by Rolleri (2004) a large degree of synonymization was suggested, with which we do not agree.

In recent years, it has become obvious that information on characters such as plant habit, rhizome morphology and leaf colour are useful, and often necessary, in identifying *Danaea* specimens to the correct species (Tuomisto & Moran, 2001). Unfortunately, characters like habit and colour are not easily preserved through the process of pressing and drying, which complicates the identification of herbarium specimens of *Danaea*. Furthermore, the rhizome is cumbersome to collect and difficult to divide between several duplicates. Collecting the rhizome kills the plant in any case. Consequently, many herbarium specimens, especially those of the larger species, do not include enough rhizome to allow reconstructing its morphology. Especially historical specimens, many of which are types, do not include sufficient information about these characters, either on the specimen itself or on the accompanying label. This has made it difficult to establish the identity of various species with certainty.

To solve this problem, we have carried out field work in different parts of the neotropics. As many type localities as possible were visited to establish the identity of the type specimens. Observing the populations in the field also yields information about the natural variation in morphological characters, and hence helps in circumscribing the

species. So far, field work has been carried out in Colombia, Costa Rica, Ecuador, French Guiana, Jamaica, Peru, Puerto Rico, Suriname and the Lesser Antilles. Future phylogenetic and systematic studies will hopefully give a greater insight in the diversity and relationships between the species of *Danaea*.

DISTRIBUTION AND ECOLOGY OF *DANAEA*

Danaea occurs solely in the New World tropics. It can be found from Mexico, through all of Central and South America, south to Bolivia. It also occurs on all Greater Antilles, and the wetter, higher islands of the Lesser Antilles. There are isolated populations in Atlantic south-eastern Brazil, southern Paraguay and Cocos Island (Costa Rica). The biogeographical patterns of *Danaea* are presently being studied.

Danaea occurs mainly in permanently wet forests on well drained soils. Several species seem to prefer steep slopes or creek banks. *Danaea* is mostly found in undisturbed rainforests, although some species tolerate disturbance, and some species even seem to favour recently disturbed places like shady wet roadside banks. *Danaea* species can be found in lowland rainforests, up to an elevation of about 2000 m in montane cloud forest and elfin woodland, but most species are found between about 300 and 1000 m elevation. In Amazonian lowland rain forests, it has been found that different species grow on soils with different nutrient status (Tuomisto & Poulsen 1996).

THE THREE MAJOR GROUPS IN *DANAEA*

Based on morphological characters, we divide *Danaea* into three major groups. This division is still tentative, as the groups overlap in some of the characters, and some species cannot be unambiguously allocated to a group. This division does not follow any of the sections proposed by Presl (1845), and the phylogenetic relationships between the species are not yet known although they are being studied.

The first group consists of species that resemble *Danaea nodosa* and are often identified as such in herbaria. These are large-statured species whose adults often exceed 1.5 m in height. Most species are characterized by a creeping rhizome (except *D. erecta* Tuomisto & R.C.Moran), the absence of nodes on the stipes (except *D. media* Liebm.), and the presence of dentations at pinna apices (except *D. erecta* and *D. grandifolia* Underw.).

The second group consists of species supposedly related to *Danaea leprieurii* Kunze. This group of species has previously been united under the name *D. elliptica* (see below). These are species of intermediate stature, 0.4-1.5 m in height. This group is characterized by erect, radially symmetric rhizomes, stipes articulated with swollen nodes (nodes sometimes lacking in *D. bipinnata* Tuomisto) and entire pinna apices. The apical pinna is always present, never replaced by an apical bud.

The third group consists of species resembling *Danaea alata* Sm, *D. moritziana* C.Presl and *D. mazeana* Underw.. These are species of small to intermediate stature, 0.1-1.5 m in height, and are characterized by radially symmetric (rarely dorsiventral) rhizomes that can be erect, creeping or ascending. The stipes are nodose, the blade usually bares many crowded pinnae, and the pinna apices are (coarsely) serrate. Some of the smaller species have translucent pinnae (*D. trichomanoides* T.Moore ex Spruce, *D. imbricata* Tuomisto & R.C.Moran, *D. tenera* C.V.Morton), and many species have bicolorous fronds, with the abaxial side pale green or whitish. The apical pinna can be replaced by a proliferous bud, but this does not seem to be a distinguishing feature

between species. To distinguish species within this group, Underwood used mostly characters of the venation, which is, in most cases, also highly variable.

Notes on the *Danaea nodosa* group

Danaea nodosa, the type species of the genus, has always been considered to be widespread, occurring throughout the range of the genus. However, recent field studies and close study of herbarium material have revealed, that the name has been applied to several clearly separate species. Often these species have different ecological preferences.

The lectotype of *Danaea nodosa* is a plate in Plumier (1705), which is based on material either collected "between Morne Rouge and Saint Pierre, Martinique" or "Port-de-Paix, Haiti". The latter locality was selected as the type locality by Underwood (1909). This was a fortunate choice, because the material we have seen from Haiti agrees with the type illustration very well: the plants have slender, dorsiventral rhizomes with two rows of leaf scars, and the pinnae are long and parallel-sided. In contrast, the plants that grow on Martinique do not match the type illustration: they have very bulky rhizomes with fronds arranged in several rows, and their pinnae are narrower and more tapering. It is obvious that the populations on the two islands represent two different species (Christenhusz, in press).

In Jamaica, most of the plants we have seen agree very well with the material from Haiti, and can thus be considered true *Danaea nodosa*. However, we found that leaf dissection in Jamaican plants varied from the normal once pinnate to fully bipinnate (*Christenhusz & Tuomisto* 3194 (IJ, TUR, UCWI). In some populations, the tendency to bipinnate fronds was stronger than in others, but in all populations where bipinnate fronds were found, once pinnate fronds were also present. No other differences were found between the once and twice pinnate fronds than the degree of leaf dissection. It seems obvious, therefore, that this is a case of within-species variation. An interesting question concerns the identity of the South American material. We have observed some differences in pinna shape between the Jamaican and South American populations, but their rhizomes and habit are similar. Even though we have never observed any tendency towards bipinnate leaf dissection in any South American population, for the time being we consider these as *D. nodosa*.

Field work in Western Amazonia has shown that *Danaea nodosa* grows on relatively nutrient-rich, clayey soils. Its juveniles have simple fronds only when very small, and the fronds become pinnate usually when they are still less than 10 cm long. A very similar plant but with cartilaginous pinna margins has been found on poorer, more loamy soils. This species has larger pinnae, especially at the juvenile stage when fronds often remain simple until they exceed 30 cm in length (Tuomisto & Groot, 1995, Tuomisto & Moran, 2001). On the basis of a photograph of one of the isotypes, the latter species was identified as *D. ulei* H.Christ. Unfortunately, other isotypes of *D. ulei* show clearly that the rhizomes in this species are erect, indicating that it belongs to the *D. leprieurii* group. Its pinna margins are not cartilaginous, either. Consequently, the poor-soil segregate of *D. nodosa* needs a new name (Christenhusz & Tuomisto, in press).

In Costa Rica, populations of supposed *Danaea nodosa* were found to be variable in whether the stipe is nodose or not. Juveniles usually had one or two nodes, but older fronds more often had none. The presence of nodes was variable even in fronds on the same rhizome, which shows that the two forms belong to the same species. These plants

have previously been identified either as *D. nodosa* or as *D. elliptica*, depending on whether nodes were present or not, as this has traditionally been the most important diagnostic character between the two species. Since true *D. nodosa* never has nodes, the names that can be applied to this species are *D. media* Liebm. and *D. elata* Liebm. *Danaea media* was described on the basis of small plants (with nodes) and *D. elata* on the basis of a large specimen (without nodes) from the same population in Mexico. These names have earlier been synonymized with *D. elliptica* and *D. nodosa*, respectively, but our observations indicate that they represent another taxon worthy of recognition at species level. We propose that the name *D. media* is used as the valid name for this species, because this epithet refers to the species having intermediate characters between the *D. nodosa* and *D. leprieurii* groups.

Notes on the *Danaea leprieurii* group

Most of the species in this group have at some stage been identified as *Danaea elliptica* Sm. in Rees, which has been considered a wide-spread and common species. The identity and typification of *D. elliptica* has however long been in turmoil. The lectotype designated by Proctor (1977) is: Jamaica, Mount Diablo, Herb. Sloane 1: 85 (BM-SL). It has been observed repeatedly that this specimen is actually a juvenile of *D. nodosa* (L.) Sm (e.g., Lellinger 2000, Tuomisto & Moran 2001). We have confirmed this by visiting Mount Diablo, where we only found individuals of *D. nodosa*. The issue of the synonymization of *D. elliptica* is discussed in more detail in Christenhusz & Tuomisto (in press).

As mentioned above, Underwood selected Haiti rather than Martinique as the type locality of *Danaea nodosa*. It is worth mentioning that since the two islands have different species of the *D. nodosa* group, the situation would now be very different had Underwood selected the other way round. If Martinique were the type locality, *D. nodosa* would be represented by a type illustration that matches the species occurring on that island rather poorly, and *D. elliptica* would become the valid name for the species that has so far been known as *D. nodosa* in the Greater Antilles and South America, which would be very confusing.

Due to the problems with the name *D. elliptica*, we call the present group of species the *D. leprieurii* group, as this is one of the oldest accepted names in this group. This group includes many apparently closely related species that are morphologically quite similar, but grow on different soil types and/or altitudes.

Danaea leprieurii was described from French Guiana, but recently also material from western Amazonia has been allocated to this species. (Tuomisto & Moran 2001). In western Amazonia, *D. leprieurii* grows on relatively poor substrates, whereas the recently described and morphologically rather similar *D. bipinnata* grows on richer soils. The two can be distinguished by size (*D. leprieurii* is smaller), the number of nodes on the stipes (2-3 in *D. leprieurii*, 0-1 in *D. bipinnata*), and usually the degree of lamina dissection. *Danaea bipinnata* was described from lowland Amazonia, but it is very similar to *D. elliptica* Sm. var. *crispula* Rosenst, which was described from lower montane elevations in the Peruvian Andes. However, *D. elliptica* var. *crispula* is never bipinnate, and it is usually larger than *D. bipinnata*.

Danaea simplicifolia Rudge is confined to the Guiana shield, and can easily be recognized by its simple fronds. The only other species with simple fronds is *D. carillensis* H.Christ, an endemic of Costa Rica, with a nodose stipe, creeping rhizome and apical dentations, and therefore belonging to the *D. alata* group. *D. simplicifolia*

only has a single node below its simple blade. From this node, sometimes one or two lateral pinnae are produced (French Guiana: *Christenhusz* 2325 (CAY, TUR), *Christenhusz* 2415 (CAY, TUR)). It then resembles *D. trifoliata* Rchb., a species that can be distinguished by its nodose stipe. Another character that distinguishes *D. simplicifolia* from juvenile *Danaea* that have not developed lateral pinnae yet, are the white abaxial surfaces of the blades, an uncommon feature in this group. It is only found in some representatives of the *D. alata* group and in the Ecuadorian *D. bicolor* Tuomisto & R.C.Moran.

Notes on the *Danaea alata* group

Danaea alata Sm. is a species confined to the Lesser Antilles (lectotype from Martinique, Plumier 1705). It is recognized by simple, widely spaced veins, nodose stipes, creeping, radial rhizomes and coarse apical dentations. Its synonyms are *D. fendleri* Underw. (Trinidad) and *D. stenophylla* Kunze (Guadeloupe).

At a first glance the closely related *Danaea mazeana* Underw. appears to be confined to Guadeloupe, but material from other Antilles is very variable. *D. mazeana* fits well within the variation of *D. jamaicensis* Underw., and cannot be consistently separated from it. However, *D. jamaicensis* sometimes has apical proliferations, which are never found in *D. mazeana*. This might be due to possible hybridization with *D. jenmanii* Underw. on Jamaica. *D. mazeana* differs in ecology from *D. alata*, as the former is confined to cloud forests above 600 m, whereas the latter is found only in rainforests at lower altitudes.

On present evidence, *Danaea jenmanii* and *D. wrightii* Underw. are conspecific. The type of *D. wrightii* is somewhat scalier, but all other characters overlap. Field work in Jamaica showed that the scalyness of *D. jenmanii* is variable. Because *D. jenmanii* has been applied more widely than *D. wrightii*, the first is proposed here for conservation over the latter. Both species were described in the same publication.

CONCLUSIONS

Field work and herbarium studies have shown that the diversity of *Danaea* is much greater than previously assumed. The first indication of this tendency was the Ecuadorian treatment (Tuomisto and Moran 2001) where 18 species were included, eight of which were described as new. The same tendency is continuing in other areas, and we now have several species in publication (Christenhusz, in press; Christenhusz & Tuomisto, in press). It seems obvious that the concepts of the geographical distribution ranges of the species will have to be changed once the taxonomy of the genus has been sorted out. More species than expected seem to have rather narrow ranges.

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TEMPORAL VARIATION IN SPOROPHYTE FERTILITY IN *DRYOPTERIS INTERMEDIA* AND *POLYSTICHUM ACROSTICHOIDES* (DRYOPTERIDACEAE: PTERIDOPHYTA)

J.M. SHARPE
SHARPLEX Services, PO Box 499, Edgecomb, Maine 04556 USA

Key words: annual variation, demography, fern, *Dryopteris intermedia,* crown fertility, plant fertility, growth, *Polystichum acrostichoides,* pteridophyte, temperate zone

ABSTRACT

A long-term demographic study to assess temporal variation in two common New England ferns, *Dryopteris intermedia* (Evergreen wood fern) and *Polystichum acrostichoides* (Christmas fern) focused on fertile leaf production by the reproductively mature sporophyte. Over an eight-year period only 29.9% of the leaves in a *D. intermedia* crown were fertile, while for *P. acrostichoides* significantly more (48.0%) of the leaves in the crown were fertile. Annual values of the percentage of plants with fertile leaves for *D. intermedia* ranged from 42% to 77% and for *P. acrostichoides* from 57% to 93% reflecting significant annual variation, possibly related to winter weather conditions. Only 16% of *D. intermedia* and 14% of *P. acrostichoides* sporophytes were fertile every year of the study. Transitions from fertile plant status to sterile plant status occurred in 15% of the *D. intermedia* observations and 14% of the *P. acrostichoides* observations. For both species, when a sterile year followed a fertile year the number of leaves in the crown decreased by approximately half a leaf. Determining the causes of such high levels of variability in plant fertility will be necessary before the role of ferns in any ecosystem can be fully understood.

INTRODUCTION

Long-term monitoring of marked individuals can provide insight into the life history of a species (Harper, 1977) as well as providing a solid basis for future experimental research (Noss, 1999). Werth & Cousens (1990) emphasized the importance of long-term studies of ferns in order to understand mortality and differential fitness, and noted that very little information is available on the life spans and generation times of ferns. There have been several short-term studies of the life history of sporophytes of specific temperate understory fern species. Field research on various aspects of the temperate fern life cycle has been reported for *Blechnum spicant* (L.) Smith (Cousens, 1973, 1981), *Thelypteris dentata* (Forsskål) E. P. St. John, *Woodwardia virginica* (L.) Smith, *Osmunda regalis* L. (Bartsch & Lawrence, 1997) and *Polystichum acrostichoides* (Michaux) Schott (Greer & McCarthy, 2000). Studies exceeding 12 years in length have been conducted on selected species of *Botrychium* (Montgomery, 1990; Johnson-Groh, 1999). Sato (1990) followed leaf production for more than nine years in *Polystichum braunii* (Spenner) Fée, *P. tripteron* (Kunze) Pr.and *Dryopteris crassirhizoma* Nakai. Few other long-term studies have considered annual variation in temperate fern life history characteristics.

Of the seven fern life history classes identified by Cousens *et al.* (1988) the reproductively mature sporophyte class has the greatest impact on ecosystem processes. Spore production, controlled by the mature sporophyte, is a significant element of the

reproductive effort for ferns (Greer & McCarthy, 2000) and may also limit establishment of the next generation (Peck, 1980). Though few quantitative studies have addressed temporal variation in fertile leaf production it is assumed that most mature ferns reliably release spores every year (Sheffield 1996). Siman *et al.* (1999) state that fertility is the rule for mature individuals of most ferns but note that the genus *Pteridium* is an exception. A few short-term studies have also noted variation from this generally accepted assumption. Cousens (1988) reported that marked adult fertile plants had been observed reverting to adult sterile plant status. This was based on a study of *Woodwardia areolata* (L.) T. Moore (= *Lorinseria areolata* (L.) C. Presl.) which lasted 30 months (Cousens, *et al.*, 1988). Sato (1990) used counts of number of veins off the leaf midrib (NV) to assess chronological age. He observed a year-to year decrease in NV in about 20% of comparisons of overwintered leaves to the newly emerged leaf cohort in individuals of *D. crassirhizoma* and *P. tripteron*, but not in *P. braunii*. Greer & McCarthy (2000) found that not all reproductively mature individuals of *P. acrostichoides* produced at least one fertile leaf in each of the two years of their study.

This exploratory study of the reproductively mature sporophyte of two temperate species was undertaken to extend our knowledge of annual variation in plant fertility in a long-term study lasting eight years. The goals were to 1) determine what percentage of the leaves produced by an individual each year were fertile, 2) assess the number of plants in a sample population that produced at least one fertile leaf from year to year, 3) examine levels of consistency in the annual sequence of fertile and sterile leaf production, 4) compare patterns of temporal variation for two different species, and 5) compare any observed temporal patterns to relatively short term local climate parameters.

STUDY SPECIES

Two temperate ferns common in northeastern forests of the USA were chosen for comparative study: *Dryopteris intermedia* (Willdenow) A. Gray, the Evergreen wood fern, and *Polystichum acrostichoides*, the Christmas fern. Leaves of *D. intermedia* are described as monomorphic by Montgomery & Wagner (1993) while those of *P. achrostichoides* exhibit strong sterile-fertile leaf dimorphism, with the fertile leaf exhibiting a distinctive terminal segment of spore-bearing leaflets that are greatly reduced in size compared to the proximal sterile leaflets (Wagner, 1993). Both species have short internodes so that the leaves form a distinctly tufted crown around the shoot apex.

MATERIALS AND METHODS

Sporophyte fertility was observed over an eight-year period from 1993 to 2000 in a secondary, mixed-hardwood forest approximately 15 m above sea level in the town of Dresden, Lincoln County, Maine (USA) using methods developed for long-term studies of fern demography in a tropical forest at the Luquillo Long Term Ecological Research site in Puerto Rico (Sharpe, 1997). The sample population consisted of 31 individuals of *D. intermedia* and 14 individuals of *P. acrostichoides* which were considered reproductively matures as they had produced spores at least once during the eight-year study period. Of those monitored, 24 individuals of *D. intermedia* and nine individuals of *P. acrostichoides* were fertile in 1993, the first year of the study. Each plant was identified by a numbered plastic stake and a small segment of colored, plastic-covered wire attached to a leaf base and transferred annually to one of the leaves in the next

year's cohort of leaves. Annual observations of sporophytes were made during the last week in August to insure that all leaves had fully expanded.

All leaves in the current year cohort were counted and each leaf was classified as sterile or fertile. To calculate a crown fertility perecentage for each sporophyte, the number of fertile leaves was compared to total number of leaves in the crown. Percentage of the plants fertile each year was determined by comparing the number of plants with at least one fertile leaf present in the crown to the total number of plants observed each year. Temporal patterns of fertile leaf production were further evaluated by noting the sequence of changes in plant fertility status, observed seven times within the eight-year monitoring period for each plant. Year-to-year transitions in plant fertility status were classified as FF (fertile to fertile), SS (sterile to sterile), FS (fertile to sterile) and SF (sterile to fertile). These categories are illustrated with an example of an individual plant which happened to experience all four types of plant fertility transitions (Figure 1). The number of continuous years a plant was sterile following and preceding a fertile year was also noted.

In order to evaluate whether relatively short term weather patterns could have an effect on plant growth, values for mean daily minimum and maximum temperatures, precipitation and snowfall were taken from records of the NOAA weather station located within 100 km of the study site in Portland Maine. Climate data were analyzed separately for summer (May through October) and winter (November through April). These analyses did not show significant variation in mean daily summer temperatures and precipitation. However, winter temperatures had significantly lower mean daily minimums in 1994 and 1996. Snowfall was significantly higher in the winter of 1996. Furthermore, there was a major cyclic disturbance in the form of an ice storm in

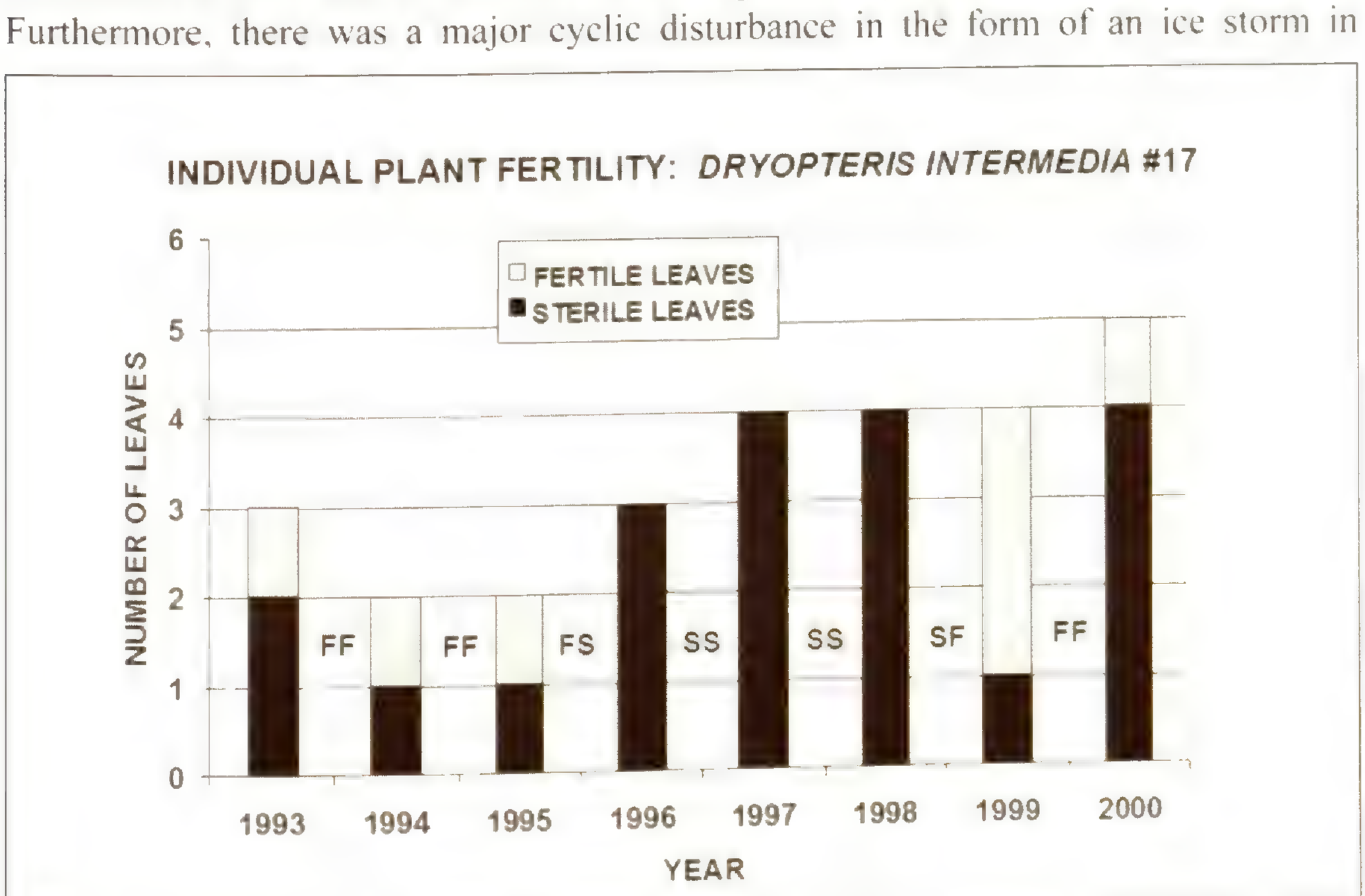

Figure 1. Profile of the fertile and sterile leaves present in the crown of a sample individual (#17) of *Dryopteris intermedia* for each of the eight years the plant was monitored. Plant fertility status transitions are noted between bars (SS = Sterile Sterile, SF = Sterile/Fertile, FF = Fertile Fertile, FS = Fertile Sterile) for this sporophyte which happened to experience all four of the possible year-to-year transitions.

February 1998 (Darwin *et al.*, 2004).

Data analysis

Means and standard error of the means (SE) were calculated for crown fertility for each plant using data collected each year (N = 8). Standard error of the means were chosen to show variation because of the small sample sizes. All percentages were arcsine transformed before statistical tests were applied. To factor out variability among marked individuals, Repeated Measures Analysis of Variance (RMA) was used to evaluate year-to-year differences in the percent of crown fertile. A one sample t-test was used to compare plant fertility and transition type percentages from year to year for each species. Paired t-tests were used to compare the different fertility characteristics for the two species. Data were analyzed using Statistix 8 (Analytical Software, 2003).

RESULTS AND DISCUSSION

Crown fertility

In eight years of monitoring these populations, observations of crowns that were composed entirely of fertile leaves were unusual for both species. Of 360 individual annual flushes of leaves observed in this study, only eight individual leaf cohorts of *Dryopteris intermedia* and 18 of *Polystichum acrostichoides* were completely fertile. Fewer than half the leaves produced by these reproductively mature plants were fertile and the mean percentage of leaves in the crown that were fertile is significantly lower for *D. intermedia* than for *P. acrostichoides* (Table 1). Neither species in this study approached 100% fertile leaf production. This could be a function of the chronological age of these plants, which is unknown. If they are all relatively young plants, perhaps the ability to produce a full cohort of fertile leaves had not yet occurred. If they are all relatively old plants, then possibly the ability to produce a full cohort of fertile leaves had been lost. Although no increasing or decreasing pattern can be seen by comparing the percentages from year to year, perhaps eight years is too small a segment of the total life span to observe such patterns. It is also possible that full fertile leaf production is not possible in the specific habitat where these plants were growing. It is possible that each species has an intrinsic limit on fertile leaf production by reproductively mature plants which integrates its habitat requirements and need for vegetative support tissue. While there are reports of high percentages of crown fertility in some temperate ferns, for example in *Leptopteris hymenophylloides* (Sussex, 1958), low crown fertility has also been observed in *Matteuccia struthiopteris* (Von Aderkas & Green, 1986). In a study undertaken in southern Siberia, Gureyeva (2001) found that environmental factors may severely limit spore production by ferns and Cousens (1973) noted population differences in fertile leaf production by *Blechnum spicant*.

There were year-to-year differences in crown fertility. The annual mean percentage of leaves that were fertile within the crown ranged from 21.9% to 38.9% for *D. intermedia* and from 37.6% to 60.6% for *P. acrostichoides* with little concordance between species in the pattern of annual increases and decreases (Table 1). *Dryopteris intermedia* had the highest total fertile leaf production in 1994 following one of the two coldest winters of the study and had the lowest total fertile leaf production following the ice storm in 1998. In contrast, *P. acrostichoides* had the lowest fertile leaf production in 1996 following one of the two coldest winters of the study and exhibited no unusual response after the ice storm. Investigations into the specific triggers for fertile leaf production have been recommended by Wagner & Wagner (1977) and could identify potential environmental factors involved. For example, it has been

TABLE 1. Summary of annual variation in crown and plant fertility for reproductively mature sporophytes of *Dryopteris intermedia* and *Polystichum acrostichoides*. N is the number of plants measured. One-sample t-tests are used to compare years for percentage of plants and transition type percentages. Repeated measures analysis of variance is used to compare years for individual percentage of crowns fertile. Paired t-test is used to compare the year-to-year differences between species. Significant differences are indicated by * ($P < 0.0500$), ** ($P < 0.0100$) and *** ($P < 0.0010$).

Year	Fertile leaves in crown		Percentage of plants fertile	Transition type percentages			
	N	Percentage of crown (mean)		SS	SF	FF	FS
Dryopteris intermedia							
1993	31	35.1±4.87%	77%	–	–	–	–
1994	31	38.9±5.88%	71%	10%	13%	58%	19%
1995	31	33.9±5.09%	71%	13%	16%	55%	16%
1996	31	22.9±5.11%	48%	23%	7%	42%	29%
1997	31	35.1±4.63%	77%	23%	29%	48%	0%
1998	31	21.9±5.35%	42%	23%	0%	42%	36%
1999	31	23.8±4.58%	55%	39%	19%	36%	7%
2000	31	27.3±4.12%	68%	26%	19%	48%	7%
All	248	29.9±1.68%	64%	22%	15%	47%	15%
F/t		F = 1.88	t = 11.52	t = 6.11	4.10	14.49	3.28
df		7	7	6	6	6	6
P		0.0748	<0.0001 ***	0.0009 ***	0.0063 **	<0.0000 ***	0.1637
Polystichum acrostichoides							
1993	14	49.6±10.64%	64%	–	–	–	–
1994	14	41.4±9.73%	71%	23%	23%	46%	23%
1995	14	44.2±10.85%	71%	15%	15%	54%	15%
1996	14	37.6±11.99%	57%	33%	0%	58%	8%
1997	14	50.4±11.28%	71%	17%	25%	50%	8%
1998	14	52.7±10.27%	79%	14%	21%	57%	7%
1999	14	60.6±9.14%	93%	0%	21%	71%	7%
2000	14	47.4±9.01%	71%	0%	7%	64%	29%
All	112	48.0±1.71%	72%	12%	16%	58%	14%
F/t		F = 0.56	t = 12.97	t = 2.84	4.57	15.22	4.19
df		7	7	6	6	6	6
P		0.7891	<0.0001 ***	0.0295 *	0.0038 **	<0.0000 ***	0.0057 **
Species comparisons							
t		-4.57	-1.22	1.22	-0.31	-1.76	0.38
df		7	7	6	6	6	6
P		0.0026 **	0.2603	0.2696	0.7702	0.1298	0.7186

demonstrated in greenhouse studies (Siman & Sheffield, 2002) that under field conditions individuals do not necessarily produce the maximum number of fertile leaves possible each year. In a year-long study of *Polypodium vulgare* L. in the United Kingdom, field-grown and greenhouse-grown plants from identical genetic stock were compared by Siman & Sheffield (2002). The indoor population showed a four-fold increase in new leaves, mostly fertile, emerging in a wave pattern thought to represent three annual cohorts for field grown plants as compared to the outdoor population. There do appear to be limits to fertile leaf production which may be consistent within species over an extended period of time. Experiments similar to this one done by Siman & Sheffield (2002) would confirm these limitations.

Plant fertility

Of 248 individual leaf cohorts of *D. intermedia* observed during the eight years of the study, 64% included at least one fertile leaf, while for 112 cohorts of *P. acrostichoides* the percentage was 72% (Table 1). The percentage of plants in the population that produced at least one fertile leaf each year ranged from a low of 42% in 1998 to a high of 77% in 1993 for *D. intermedia,* a range from the lowest year to the highest of 35%, reflecting significant year-to-year variation. For *P. acrostichoides* there were also significant year-to-year differences, with a range from the lowest year (1996) to the highest year (1999) of 36% (Table 1). For *D. intermedia,* the lowest percentage of plant fertility occurred following the ice storm. A paired comparison of annual plant fertility percentages did not detect a significant difference between the two species (Table 1).

Annual sequence of plant fertility status

There are some elements of life history than can only be determined by making repeated observations of marked individuals over a long period of time. One of those elements is the year-to-year change in an individual sporophyte's fertility status. Overall, a plant was sterile one year as well as the next (SS) 48 times in the 217 observations of transition for *D. intermedia* (Table 1). Of these SS transitions, 9 (3 plants) occurred before a plant produced its first fertile leaf while for all others (81%) the SS transition occurred after the plant had produced at least one fertile leaf. For *P. acrostichoides*, SS transitions occurred 11 times out of 98 transition observations, with one plant (of 14) accounting for all of the SS transitions that occurred before a fertile leaf was produced. Thus 89% of the SS transitions for *P. acrostichoides* occurred after a fertile leaf had been produced. Sterile to fertile (SF) transitions occurred in 15% of the *D. intermedia* observations and 16% of the *P. acrostichoides* observations (Table 1).

Fertile to fertile (FF) transitions occurred in 47% of the *D. intermedia* observations and 58% of the *P. acrostichoides* observations (Table 1). A small percentages of all *D. intermedia* plants observed produced fertile leaves only once or twice, while all *P. acrostichoides* individuals produced at least one fertile leaf during three or more years (Table 2A). Although all plants in this study were reproductively mature, only 16% of the individuals of *D. intermedia* and 14% of the individuals of *P. achrostichoides* produced at least one fertile leaf during each of the eight years of the study (Table 2A). Of the sporophytes of *D. intermedia* which were fertile at the start of the study in 1993, 75% were fertile in 1994 while only 21% were consistently fertile through 2000, the last year of the study (Table 2B). Of the sporophytes of *P. acrostichoides* which were fertile in 1993, 67% were fertile in 1994, compared to the 60.8% sequential reproducers observed in a two-year study of this species in southeastern Ohio by Greer & McCarthy (2000). By 2000, only 22% of the *P. acrostichoides* the individuals that were fertile in 1993 could be called sequential reproducers. Thus, as the number of years a plant is

monitored increased, the percentage of sequential reproducers decreased at approximately the same rate for both species (Table 2B).

Fertile to sterile transitions (FS) reverse the more common trend of fertile-to-fertile transitions in the chronological maturation of a reproductively mature sporophyte described by Sheffield (1996). However, plants that were fertile one year and produced

TABLE 2. Comparison of fertility and sterility frequencies for reproductively mature sporophytes of *D. intermedia* and *P. acrostichoides* observed for an eight-year period from 1993 to 2000. Table A includes all plants which became fertile during the eight-year monitoring period. Table B includes only plants which were fertile in 1993.

Years	*D. intermedia*	*P. acrostichoides*
A. Number of years that individuals are fertile		
1	7%	0%
2	3%	0%
3	16%	21%
4	12%	7%
5	16%	21%
6	19%	14%
7	9%	21%
8	16%	14%
B. Number of consecutive years that fertile individuals remain fertile		
1	100%	100%
2	75%	67%
3	63%	67%
4	38%	56%
5	38%	56%
6	29%	44%
7	25%	44%
8	21%	22%
C. Number of fertile/sterile transitions per individual		
1	54%	50%
2	32%	37%
3	14%	13%
D. Span of sterile years after and before a fertile year		
1	60%	60%
2	20%	20%
3	8%	10%
4	8%	10%
5	4%	0%

no fertile leaves the next year (FS) were seen in 15% of the *D. intermedia* observations and 14% of the *P. acrostichoides* transition observations. For *D. intermedia*, 70% of the individuals reverted to sterile status from fertile status (FS) at least once during the eight-year monitoring period, while 57% of *P. acrostichoides* individuals had FS transitions. For approximately half of the plants of both species an FS transition occurred only once (Table 2C). Given that a plant must transition back to fertile status in order to become sterile again, the maximum number of FS transitions possible in an eight-year study is three. This maximum number of FS transitions was noted for 14% of the observations for *D. intermedia* and 13% of the FS observations for *P. acrostichoides*. The span of years that a previously fertile sporophyte remained sterile ranged from one to five for *D. intermedia* and one to four for *P. acrostichoides* (Table 2D). For both species the majority (60%) remained sterile for only one year (Table 2D). Of the FS transitions for *Dryopteris intermedia* (Table 1), most occurred in 1998 (36%), following the ice storm and in 1996 (29%), following a winter with very low daily minimum temperatures (Table 1). For *P. acrostichoides* most FS transitions (29%) occurred in 2000 (Table 1).

Crown size and changes plant fertility status

Changes in crown size can be related to the annual transitions to and from fertile leaf production. Plants maintained a stable crown size following FF transitions (Table 3). Crown size was also stable for SS transitions for *D. intermedia*, though it increased for *P. acrostichoides*. However, following FS transitions, individual plants produce a significantly smaller sterile crown by over half a leaf (Table 3). Following SF transitions, the increase in the size of the fertile crown is also significant for *D. intermedia*, with an increase in *P. acrostichoides* as well (Table 3). Thus, even for the same individuals, the number of leaves in the crown increases with a shift from plant sterility to fertility. On a smaller scale than that observed experimentally by Siman & Sheffield (2002), it appears that when field conditions favor above-average fertile leaf production for *D. intermedia* and *P. acrostichoides*, more leaves are produced.

TABLE 3. Comparison of changes in crown sizes for transitions in plant fertility status from one year to the next. Significant differences are indicated by * ($P < 0.0500$) and ** ($P < 0.0100$).

Transition	*Dryopteris intermedia*				*Polystichum acrostichoides*			
	N	Mean difference	t	P	N	Mean difference	t	P
Fertile/Fertile	101	-0.040±0.186	-0.21	0.8314	53	-0.076±0.294	0.26	0.7982
Sterile/Sterile	48	-0.021±0.210	-2.25	0.0308*	11	+0.727±0.304	-1.13	0.2793
Fertile/Sterile	35	-0.571±0.254	3.20	0.0031**	13	-0.539±0.475	1.16	0.2654
Sterile/Fertile	33	+0.727±0.227	-0.10	0.9212	15	+0.333±0.287	2.39	0.0379*
Min/Max		-4/+6				-7/+5		
F		3.57				1.12		
P		0.0149*				0.3438		

CONCLUSIONS

The most striking observations to emerge from this temporal study of annual variation in individual plant fertility are 1) the overall low level of fertile leaf production in both species with very few observations of whole crown fertility, 2) the inconsistency of the percentage of the crown which is fertile from year to year, 3) significant differences in the number of plants that are fertile from year to year for each species, a phenomenon possibly linked to winter weather conditions, 4) the difference between species in the overall percentage of plants that are fertile 5) the similarities between species with respect to the annual patterns in changes of the percentages of fertile plants and transitions in plant fertility status 6) the significant year-to-year variation in the percent of the population that experiences a fertile to fertile plant status transition, 7) expansion of individual crown size when fertile leaves are produced, and reduction of crown size when a fertile plant fails to produce fertile leaves the following year. Most of these characteristics of fertile leaf production could not have been known without annual monitoring of marked individuals. Though eight years seems to be a relatively short time compared to the life span of long-lived sporophytes, it was possible to quantify several previously untested assumptions about sporophyte growth.

The original intention of this study was to determine if annual variability in plant fertility could be detected in field populations of sporophytes of temperate species. With the exception of general observations relating to significant local weather patterns, no attempt was made to determine the cause of any observed variation. It is certainly clear from these results that there can be a high level of annual variability in fertile leaf production in temperate ferns. It is also clear that observing a sporophyte only once can lead to a number of erroneous assumptions about its past life history status. A plant with no fertile leaves cannot automatically be assumed to be an immature plant. A plant with one fertile leaf may or may not have been producing fertile leaves longer than one with a 100% fertile crown. A plant that is fertile may or may not be fertile the following year. A population that has the same proportion of fertile plants from one year to the next may still reflect numerous changes due to independent changes in the fertility status of individual plants. While the two species chosen for observation in this study may differ in the overall number and timing of fertile leaves produced, there was a striking similarity in the frequency of the different types of year-to-year transitions in plant fertility status.

Fundamental to understanding of all of these observations is a knowledge of the specific process that determines whether an emergent leaf will be fertile or sterile (White 1971). The current exploratory study, limited as it was to simply observing the reproductive sporophyte, has provided few clues about the stimuli behind the observed patterns. The differences between species detected in this long-term field study of just two species indicate that for each species the fertility triggers may be different. Significant year-to-year variation in plant fertility suggests that environmental factors may be important. Annual variation may be related to climate factors but the relatively short time span of the study and the many potential microhabitat influences require experiments to properly assess these observations.

More long-term field studies are needed as the differences between these two species suggest that the patterns of leaf and plant fertility can vary widely. Because the limitations on observing plants in the field were unknown at the start of this study. sample sizes of plants for which data was available for all eight years were small by the

end of the study, especially for *P. acrostichoides*. The number of plant fertility transitions from fertile to sterile taking place after a plant had become reproductively mature could only be observed a maximum of three times in an eight-year period, limiting the potential for identifying underlying causes. Only one large cyclic event occurred during the study, limiting the potential for generalizations about disturbance effects.

The length of study was limited because of the choice of study site. It was conducted on private land which changed hands after eight years and was no longer accessible for research. For long-lived perennials, a long-term study should encompass a large part of the life span of a sporophyte, and should ideally extend to 100 years or more. As indicated by Werth & Cousens (1990), a long-term study should be conducted at a site guaranteed to be in place for the long-term. The Long Term Ecological Research (LTER) program (Van Cleve & Martin 1991) which has extended world-wide from its original designation of sites in the United States can provide such stable study locations for future long-term studies. The LTER sites also provide for maintenance of standardized data sets long-term which allows for continual monitoring of marked individuals beyond the lifetime of a single individual researcher. The availability of LTER data on the internet also facilitates supplemental short-term studies and experiments based on earlier observations, another recommendation made by Werth & Cousens (1990). Long-term natural experiments such as this one rely on inference from uncontrolled climate data. Although this approach does not have the rigor of a controlled experiment, it does document variation under real environmental conditions. Another advantage of conducting both long and short term studies at an LTER is the continual monitoring of climate parameters as well as other abiotic and biotic environmental characteristics which can be related to an individual researcher's observations about ferns.

This long-term study of fertility in two wintergreen fern species from the same forest showed different patterns of annual variation, suggesting that any future ecological assumptions about ferns must account for differences among fern species. Studies of populations of both *D. intermedia* and *P. acrostichoides* throughout their ranges are needed and other life history stages could exhibit such amplitudes of annual variability as well. Long-term field monitoring and additional experimentation with other fern species will be necessary before the ecological generalizations hoped for by Harper (1982) can be made.

ACKNOWLEDGMENTS

I am grateful for the encouragement given to me by Mike Cousens many years ago. His pioneering work in fern demographic studies inspired many of the questions I have addressed. Thought-provoking discussions of fern ecology with Herb Wagner and Charlie Werth further stimulated my enthusiasm for field studies of ferns. This paper is dedicated to the memory of these three pteridologists whose insights based on field studies were incomparable.

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NEW ZEALAND *ASPLENIUM* (ASPLENIACEAE: PTERIDOPHYTA) REVISITED – DNA SEQUENCING AND AFLP FINGERPRINTING

L.R. PERRIE[1] & P.J. BROWNSEY
Museum of New Zealand Te Papa Tongarewa, P.O. Box 467, Wellington, New Zealand
(Email: [1]leonp@tepapa.govt.nz)

Key words: New Zealand, *Asplenium*, *A. hookerianum*, *A. bulbiferum*, *A. gracillimum*, *A. richardii*, chloroplast DNA sequence, AFLP DNA-fingerprinting, polyploid, hybridisation.

ABSTRACT

This paper summarises our continuing study of the evolutionary history of *Asplenium* in New Zealand. Chloroplast DNA sequence data and AFLP DNA-fingerprinting have been used to examine the origins and relationships of the New Zealand *Asplenium* taxa, to test species boundaries, and to further investigate the ancestry of the octoploid *Asplenium* taxa belonging to the Austral group.

INTRODUCTION

In 1863, after three years in New Zealand, Samuel Butler's "we have one very stupid white gentian" (Butler, 1863) was assumedly a frustrated reflection of the difficulty of recognising distinct entities within New Zealand *Gentaniella* Moench (there are actually 30 species, and only half have white flowers; Glenny, 2003). Analogous sentiments are apparent from those who first dealt taxonomically with *Asplenium* L. in New Zealand. Joseph Hooker (1855, p.33) wrote "The New Zealand kinds have defied all attempts to be limited by words". Similarly, "[some] are extremely inconstant and pass into one another, thus rendering their classification a work of considerable difficulty" (Thomson, 1882, p.72), and "The New Zealand species present exceptional difficulties to the student, on account of their extreme variability and the manner in which several of them are connected by intermediate forms" (Cheeseman, 1906, p.987). Allan (1961, p.75) stated that the species of New Zealand *Asplenium* were "very ill-defined", and that while many appeared to respond "markedly to environmental conditions...[,] there is also no doubt that hybridism plays an important part".

Indeed, hybridisation has proved to be frequent amongst (some) New Zealand *Asplenium*, and although these hybrids blur the morphological discontinuities between taxa, they are sterile and present little opportunity for introgressive gene flow (Brownsey, 1977a). The identification of hybrids was an integral part of delimiting taxa in Brownsey's (1977b) taxonomic revision of New Zealand *Asplenium*, in which 14 species and four subspecies were recognised. Since that treatment three species have been newly described (Brownsey & Jackson 1984; Brownsey, 1985; Brownsey & de Lange, 1997), some names have changed (Brownsey, 1979; Brownsey, 1999), and the appropriate rank for some taxa has been debated (Ogle, 1985; Brownsey, 1998; Perrie & Brownsey, 2005a), such that a present treatment (Table 1) might recognise 18 species and four subspecies; comprising approximately 10% of the New Zealand fern flora (Brownsey & Smith-Dodsworth, 2000).

This paper will summarise some of our recent discoveries in New Zealand *Asplenium*, but we emphasise that our understanding of the evolution of New Zealand

TABLE 1: A present taxonomic treatment of *Asplenium* in New Zealand compared with that of Brownsey (1977b).

Present Treatment	**As treated by Brownsey (1977b)**
A. appendiculatum (Labill.) C.Presl subsp. *appendiculatum*	*A. terrestre* Brownsey subsp. *terrestre*
subsp. *maritimum* (Brownsey) Brownsey	subsp. *maritimum* Brownsey
A. bulbiferum G.Forst.	*A. bulbiferum* G.Forst. subsp. *bulbiferum*
A. gracillimum Colenso	subsp. *gracillimum* (Colenso) Brownsey
A. chathamense Brownsey	-
A. cimmeriorum Brownsey et de Lange	-
A. flabellifolium Cav.	*A. flabellifolium* Cav.
A. flaccidum G.Forst. subsp. *flaccidum*	*A. flaccidum* G.Forst. subsp. *flaccidum*
subsp. *haurakiense* Brownsey	subsp. *haurakiense* Brownsey
A. hookerianum Colenso	*A. hookerianum* Colenso
A. lamprophyllum Carse	*A. lamprophyllum* Carse
A. lyallii (Hook.f.) T.Moore	*A. lyallii* (Hook.f.) T.Moore
A. oblongifolium Colenso	*A. lucidum* Forst.f.
A. obtusatum G.Forst. subsp. *obtusatum*	*A. obtusatum* G.Forst. subsp. *obtusatum*
subsp. *northlandicum* Brownsey	subsp. *northlandicum* Brownsey
A. paupereequitum Brownsey et P.J.Jacks.	-
A. polyodon G.Forst.	*A. polyodon* G.Forst.
A. richardii (Hook.f.) Hook.f.	*A. richardii* (Hook.f.) Hook.f.
A. scleroprium Hombr.	*A. scleroprium* Hombr.
A. shuttleworthianum Kunze	*A. shuttleworthianum* Kunze
A. trichomanes L. subsp. *quadrivalens* D.E.Mey emend Lovis	*A. trichomanes* L.
subsp. nov.	-

Asplenium is far from complete.

RELATIONSHIPS AND BIOGEOGRAPHY

Brownsey (1977a) considered the *Asplenium* species hybridising in New Zealand to comprise a closely related group, dubbed the 'Austral' group, and this has been supported by phylogenetic analyses of chloroplast DNA sequence data (Perrie & Brownsey, 2005a). The species in New Zealand that do not hybridise there - *A. flabellifolium*, *A. trichomanes*, *A. pauperequitum*, and *A. polyodon* - have closer affinities elsewhere (the former three with a primarily temperate, northern hemisphere group, and *A. polyodon* with a group that includes *A. aethiopicum*). Interestingly, the Austral group is closely related to the bird's nest ferns (e.g., *A. australasicum* (J.Sm.) Hook.) and the finely dissected *A. theciferum* (Kunth) Mett., which, as *Loxoscaphe thecifera* (Kunth) T.Moore, is the type of *Loxoscaphe* T.Moore.

Amongst the New Zealand members of the Austral group, three chloroplast sub-groups are clearly delimited: the Bulbiferum, Flaccidum, and Obtusatum chloroplast groups (Perrie & Brownsey, 2005a). However, it remains unclear how these groups are related to one another, as different DNA regions support conflicting relationships: {{Bul,Obt}Fla} with 71% bootstrap support from the rbcL gene, versus {{Bul,Fla}Obt} with 85% bootstrap support from the trnL-trnF intergenic spacer.

Molecular dating, using penalised likelihood of *rbc*L DNA sequence data and a calibration of 140 million years ago for the divergence of *Asplenium* and *Hymenasplenium* Hayata, recovers dates of 45 million years ago or younger for the divergence between each New Zealand *Asplenium* species and its closest non-New Zealand relative in the sample set analysed (Perrie & Brownsey, 2005a). The calibration age is probably conservatively old (for instance, Schneider *et al.* (2004) calculated the *Asplenium-Hymenasplenium* split at just 55 million years ago), so it is likely that the estimated divergence ages are (considerably) younger than actually calculated. In any case, the estimated ages of the divergence are much more recent than the geological separation of New Zealand from Gondwana (c.80 million years ago), implicating multiple events of long-distance dispersal in the origins of New Zealand *Asplenium* (Perrie & Brownsey, 2005a). The entire Austral group appears to have arisen after New Zealand's isolation. Therefore, the disjunct distributions of each of the seven Austral *Asplenium* taxa that occur in New Zealand and elsewhere requires inference of at least one dispersal event (unless the taxa are actually polyphyletic). Dispersal across the Tasman Sea (c.2000 km) is potentially so common that it would be of considerable interest to investigate the degree of genetic isolation between Australian and New Zealand populations of shared fern species.

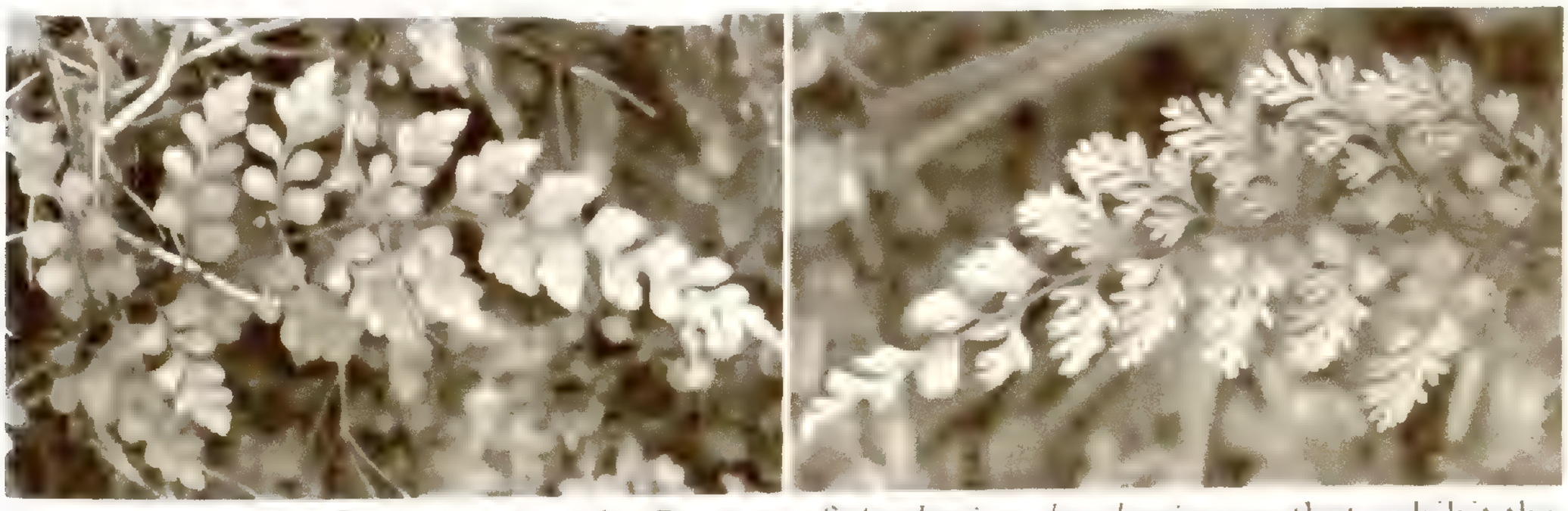

Figure 1. Plants from the Kaweka Ranges of *Asplenium hookerianum* that exhibit the broad-pinnuled and narrow-pinnuled morphology that has previously been referred to as *A. hookerianum* and *A. colensoi*, respectively.

ASPLENIUM HOOKERIANUM

AFLP DNA-fingerprinting has been used in conjunction with chloroplast DNA sequencing to investigate some groups in more detail. The morphologically distinct *Asplenium hookerianum* and *A. colensoi* were described by Colenso (1845) in the same publication; the ultimate segments are broad in the former, and narrow in the latter (Figure 1). It is quite common to find sites where both broad and narrow-pinnuled plants grow together, with few if any intermediates, thereby creating the impression of two morphologically discrete groups growing in sympatry. However, genetic variation as assayed by AFLP DNA-fingerprinting and chloroplast DNA sequencing is not concordant with the morphological variation (Perrie & Brownsey, 2005b), and indicates that only one species should be recognised (i.e., *A. hookerianum*).

ASPLENIUM BULBIFERUM

In part because of the apparent origins of *Asplenium* (*bulbiferum* subsp.) *gracillimum* discussed below, we believe that the taxa previously recognised as *A. bulbiferum* subsp. *bulbiferum* and *A. bulbiferum* subsp. *gracillimum* (Brownsey, 1977b) should be treated at the specific level as *A. bulbiferum s.s.* (hereafter simply *A. bulbiferum*) and *A. gracillimum* (Perrie & Brownsey, 2005a). Circumscribed as such, the name *A.*

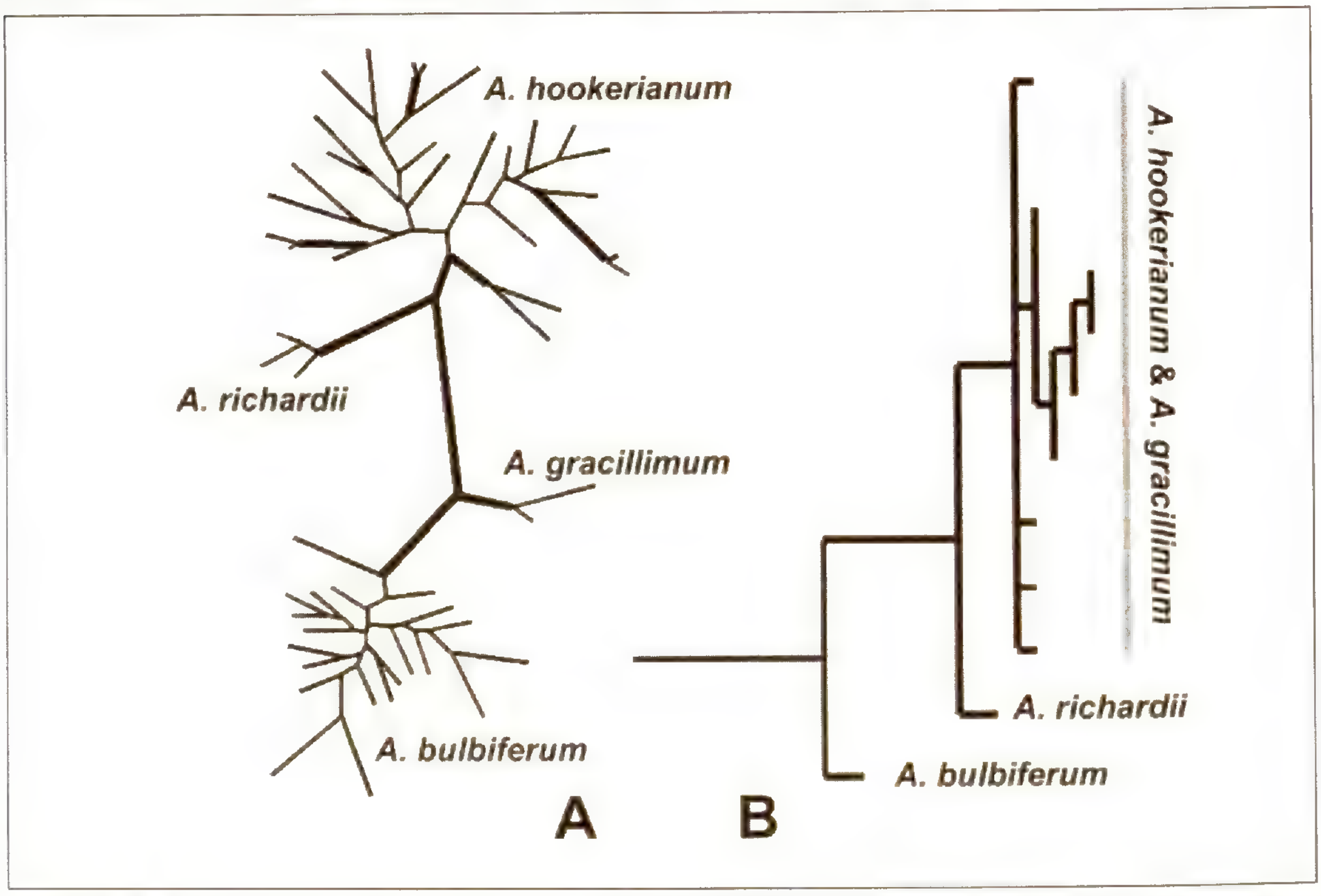

Figure 2. A: Maximum parsimony analysis of 469 AFLP characters for the tetraploids *Asplenium bulbiferum* and *A. hookerianum*, together with the octoploid *A. richardii*, a putative autopolyploid of *A. hookerianum*. Representatives from one of the *A. gracillimum* lineages are included for comparison. One of 55 most parsimonious trees, which differ in the internal arrangement of samples within *A. bulbiferum* and *A. hookerianum*. Thickened branches indicate those with >80% bootstrap support. **B:** One of three most parsimonious trees, differing in the arrangement of the *A. hookerianum* and *A. gracillimum* samples, from chloroplast *trn*L-*trn*F region DNA sequence data. Rooted using samples from the Flaccidum and Obtusatum chloroplast groups (not shown).

bulbiferum is then restricted to tetraploid plants, and is endemic to New Zealand. Further, it is quite distinct from the plant common in cultivation that is frequently labelled "*A. bulbiferum*" (Perrie *et al.*, 2005). *Asplenium bulbiferum* appears to be less genetically variable than its closest known tetraploid relative, *A. hookerianum*. Only one *trn*L-*trn*F region haplotype is presently known from *A. bulbiferum*, as opposed to eight in *A. hookerianum*. Also, only 38% of AFLP loci were polymorphic within *A. bulbiferum*, compared to 52% within *A. hookerianum*, despite more populations being sampled from the former.

ASPLENIUM GRACILLIMUM

The octoploid *Asplenium gracillimum* (previously *A. bulbiferum* subsp. *gracillimum*) appears to be an allopolyploid between the tetraploids *A. bulbiferum* and *A. hookerianum*. *Asplenium gracillimum* produces bulbils like *A. bulbiferum* (albeit with much less frequency), but has the chloroplast DNA sequence of *A. hookerianum* (Perrie & Brownsey, 2005a). Further, *A. gracillimum* is intermediate between its two putative

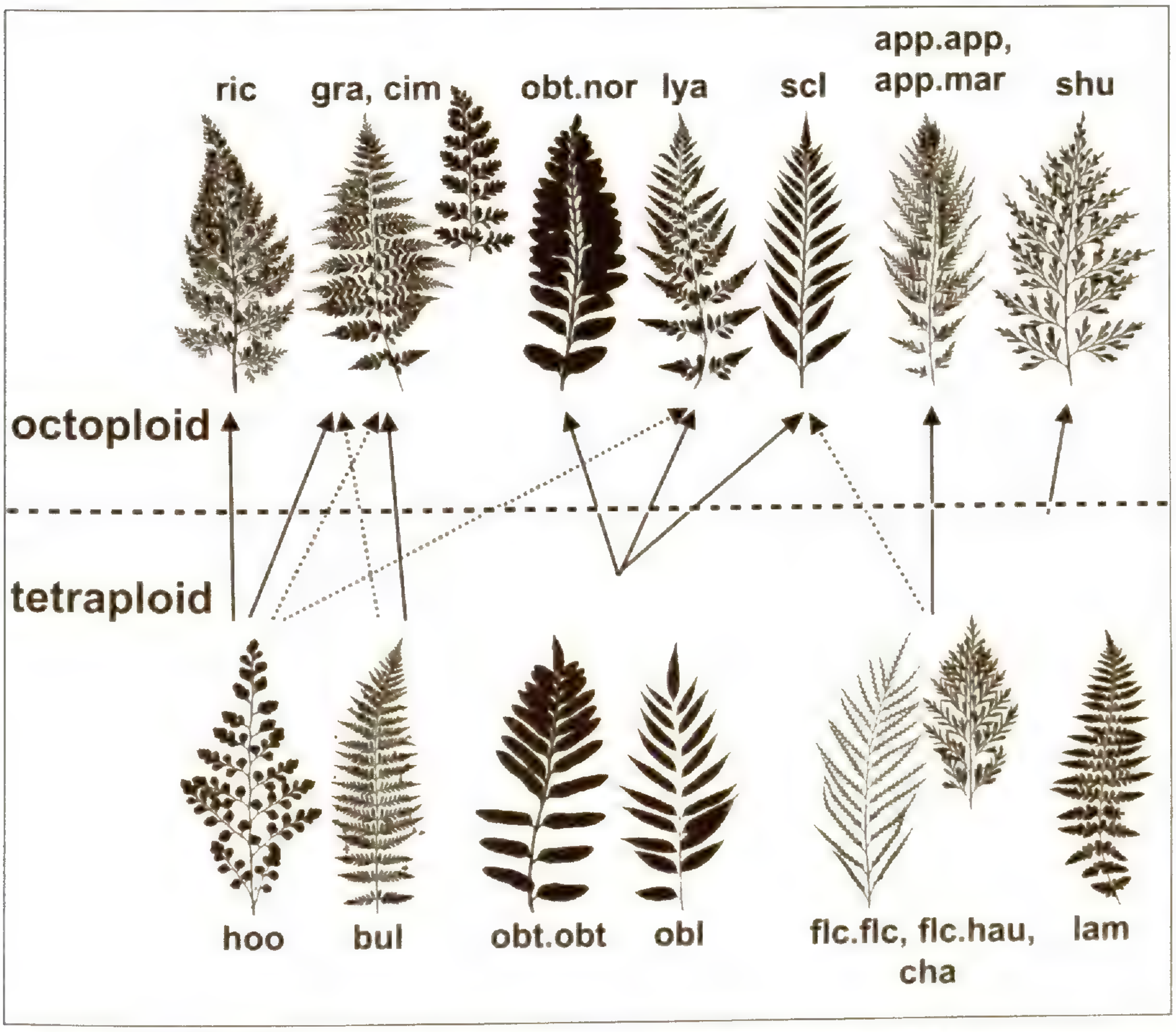

Figure 3. Hypothesised origins for the New Zealand species of the *Asplenium* Austral group. Octoploid taxa subtended by a single arrow are thought to be autopolyploids. Probable allopolyploids are subtended by two arrows. Solid arrows reflect linkages indicated by chloroplast DNA sequences; dashed arrows are linkages inferred from morphology. Arrows not pointing directly to a tetraploid taxon reflect uncertainty. Taxa are represented by the first three letters of their name in Table 1, except 'flc' = *flaccidum*. Fronds are not to scale.

parents with regards to frond architecture, scale shape, and habitat.

Reminiscent of the results of Trewick *et al.* (2002) with *Asplenium ceterach* L., chloroplast DNA sequence haplotypes shared by *Asplenium hookerianum* and *A. gracillimum* indicate that the latter has had multiple polyploid origins. Although this work is still preliminary, the different chloroplast DNA sequence haplotypes found in *A. gracillimum* appear to correspond to distinct groups detected with AFLP (Perrie & Brownsey, in prep.). Some of these apparently independently derived lineages of *A. gracillimum* appear to be sympatric, but it is unknown what happens reproductively where they meet.

ASPLENIUM CIMMERIORUM

The recently described *Asplenium cimmeriorum* has a conservation status of 'sparse', being known only from limestone regions in the north-west of the South Island and around Waitomo in the North Island (Brownsey & de Lange, 1997). Chloroplast DNA sequences indicate that the north and south populations of *A. cimmeriorum* have independent derivations; one with an *A. hookerianum*-like chloroplast and the other with an *A. bulbiferum*-like chloroplast (Perrie, de Lange, & Brownsey, in prep.). AFLP also recovers them as distinct groups (with both also distinct from *A. gracillimum*). This suggests a need to provide independent conservation assessments, with the northern Waitomo plants being much less common than those in the south.

Both groups of *Asplenium cimmeriorum* appear to be allopolyploids between *A. bulbiferum* and *A. hookerianum* (like *A. gracillimum*). This situation presents the problem of how to deal taxonomically with multiple lineages of independent but effectively equivalent origins, some of which are ecologically and/or morphologically recognisable (e.g., *A. cimmeriorum* from *A. gracillimum*) while others are not (e.g., the cryptic lineages within *A. gracillimum*).

ASPLENIUM RICHARDII

The octoploid *Asplenium richardii* is possibly an (old) autopolyploid of a narrow-pinnuled plant of *A. hookerianum*. In maximum parsimony analysis of AFLP data, *A. richardii* falls just outside the diversity found in extant *A. hookerianum*, which contrasts with the putatively allopolyploid lineages of *A. gracillimum* that lie intermediate between *A. bulbiferum* and *A. hookerianum* (Figure 2; see Perrie *et al.* (2003a) for discussion of AFLP data and type of polyploidy). The chloroplast DNA sequences of *A. richardii* are allied to, but nevertheless distinct from, those found in extant *A. hookerianum* (Figure 2). This suggests that if *A. richardii* is an autopolyploid from a narrow-pinnuled, *A. hookerianum*-like plant, then it is perhaps not of recent origin. That is, sufficient subsequent time has passed since its origin that the *A. richardii* chloroplast DNA sequences have (a) been lost from the extant populations of *A. hookerianum* and/or (b) acquired apomorphic changes.

AUSTRAL GROUP OCTOPLOID ORIGINS

Chloroplast DNA sequences have revealed the origins of the octoploid, New Zealand taxa from the Austral group with varying degrees of precision (Perrie & Brownsey, 2004, 2005a), and our present knowledge is summarised in Figure 3. For instance, *Asplenium hookerianum* and *A. gracillimum* actually share *trn*L-*trn*F region haplotypes (Perrie & Brownsey, 2005a; Perrie & Brownsey, in prep.), while more than 2000 base-pairs from four chloroplast loci are unable to differentiate between *A. oblongifolium* and

A. obtusatum subsp. *obtusatum* as the chloroplast parents of *A. lyallii* and *A. scleroprium* (Perrie & Brownsey, 2004). Some of the octoploids are thought to have autopolyploid origins: *A. appendiculatum* (from an *A. flaccidum*-like or *A. chathamense*-like progenitor), *A. obtusatum* subsp. *northlandicum* (possibly from *A. obtusatum* subsp. *obtusatum*), and *A. richardii* (see above). Others are probably allopolyploids: *A. cimmeriorum*, *A. gracillimum* (see above), *A. lyallii* (between something in the Obtusatum chloroplast group and possibly *A. hookerianum*), and *A. scleroprium* (between something in the Obtusatum chloroplast group and something like *A. flaccidum*). *Asplenium shuttleworthianum* has chloroplast DNA sequences that nest within the Flaccidum chloroplast group, but no close tetraploid is known.

CONCLUSION

The extant *Asplenium* of New Zealand are derived from disparate groups within the genus. Long-distance dispersal has seemingly played a major role in shaping the distributions of *Asplenium* in the south-west Pacific, as is the case for much of the flora of New Zealand (Winkworth *et al.* 2002; Perrie *et al.* 2003b). Genetic data has allowed the further unravelling of the histories of some of the Austral octoploids and a resolution of some taxonomic problems (e.g., *A. hookerianum*), but it also has unveiled new avenues for investigation (e.g., the multiple, cryptic groups within *A. gracillimum*). Many issues within New Zealand *Asplenium* remain to be tackled, such as clarifying the boundaries between some taxa (e.g., Perrie & Brownsey, 2004) and establishing the most appropriate ranks for others (Ogle, 1987).

ACKNOWLEDGEMENTS

We are grateful to Peter de Lange and Lara Shepherd who have collaborated with us on some aspects of this work, and to the organisers for the opportunity to contribute to the Ferns for the 21st Century conference and its proceedings. This work was funded by the Foundation for Research, Science and Technology (contract MNZX0201).

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MOLECULAR EVIDENCE FOR MULTIPLE ORIGINS OF THE APOMICTIC TRIPLOID FERN *CORNOPTERIS CHRISTENSENIANA* (WOODSIACEAE)

C.-H. PARK[1] & M. KATO[2]

[1]Laboratory of Ecology Science, Department of Biology, Faculty of Science, Kyushu University, 6-10-1, Hakozaki, Higashi-ku, Fukuoka 812-8581, Japan
Corresponding author; (Email: cparkscb@mbox.nc.kyushu-u.ac.jp)
[2]Department of Biological Sciences, Graduate School of Science, University of Tokyo, 7-3-1 Hongo, Tokyo 113-0033, Japan

Key words: apogamy, apomixis, *Cornopteris christenseniana*, hybrid fern, multiple origins, triploid

Apomixis (apogamy in a broad sense, agamospermy, agamospory) is a reproductive pathway via chromosomally unreduced spores and gametophytes and the subsequent apogamous reproduction (in a strict sense), i.e. asexual production of a sporophyte from vegetative cells of a gametophyte. Here we use the term apomixis in a broad sense and apogamy in a strict sense to avoid confusion. In pteridophytes, about 10% of the world's species and about 15% of Japanese species are apomictic. Apomixis is often associated with polyploidy, and three quarters of apomictic pteridophytes are triploid. It is often argued that apomixis, like polyploidy, plays a significant role as an escape from sterility caused by hybridization.

Although *Cornopteris christenseniana* had been believed to be a sterile triploid interspecific hybrid, our previous study showed that it produces viable spores at various frequencies and forms apogamous sporophytes at low or moderate frequencies in culture (Park & Kato, 2003). It also suggested that apomictic reproduction (in a broad sense) occurs naturally in an artificial environment in the Fern Garden of the Botanical Gardens, University of Tokyo. We have analyzed molecular variation of the nuclear and cpDNA in *C. christenseniana* and its closely related species. The results strongly support the suggestion that many plants of *C. christenseniana* propagate by apomixis in the artificial environment and not by *in situ* hybridization. We also found that plants of *C. christenseniana* that had been collected from various wild populations, had arisen independently on a markedly recurrent basis. We suggest that *Cornopteris christenseniana* is an incipient apomictic species of multiple and polytopic origin, and its apomixis is not so strongly regulated as in obligate apomicts. The multiple origins of incipient apomicts imply that the evolution of apomixis in *C. christenseniana* began with unreduced sporogenesis with a pleiotropic effect leading to subsequent apogamy.

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ISSN 0308-0838